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Garrett Evan Barr

University of New Hampshire, Durham

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THE ROLES OF BROOK TROUT AND LARVAL TWO-LINED
SALAMANDERS AS PREDATORS IN STREAMS

BY

GARRETT EVAN BARR

B.S., State University of New York at Binghamton, 1995
M.S., University of New Hampshire, 2000

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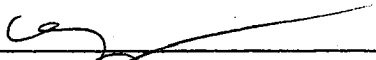
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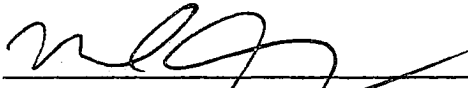
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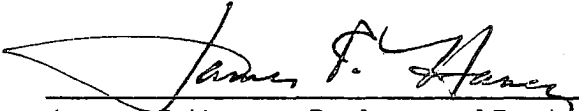
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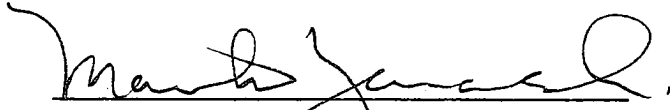
Mark J. Ducey, Associate Professor of
Forest Biometrics and Management



James F. Haney, Professor of Zoology



Thomas D. Lee, Associate Professor
of Forest Ecology



Mariko Yamasaki, Principal Research
Wildlife Biologist, USDA Forest Service,
Northern Research Station

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Date

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ABSTRACT

THE ROLES OF BROOK TROUT AND LARVAL TWO-LINED SALAMANDERS AS PREDATORS IN STREAMS

by

Garrett Evan Barr

University of New Hampshire, September 2007

To test the effects of brook trout (*Salvelinus fontinalis*) on stream macroinvertebrates and salamander larvae, I conducted a large-scale manipulation of trout presence in the White Mountain National Forest, NH. I included 9 streams in the study: 3 with trout, 3 without fish, and 3 without fish to which I added trout. I measured invertebrate benthic density before and 1 yr following trout translocation and drift density before, shortly following, and 1 yr following trout translocation. I also measured larval two-lined salamander (*Eurycea bislineata*) density and day and night activity on the stream substrate surface before and 1 yr following trout translocation.

Trout presence did not affect invertebrate benthic density, drift density, or drift periodicity; however, a few taxa reduced their drift with trout. Ordinations identified patterns in benthic invertebrates that varied

by time and space and drifting invertebrates that varied by time. Salamander density and daytime activity decreased following trout addition to streams, and salamander activity shifted from aperiodic to more nocturnal with fish.

Among the attempts to understand variation among stream predation studies are 3 models that address prey movement, prey behavior, and spatial scale. To analyze the relevance of the models, I compared the predator impact for each taxon with its propensity to drift, relative (trout vs. fishless streams) propensity to drift, and trout predation rate. I found no clear patterns. However, taxa with relatively high drift rates experienced relatively high trout predation.

In a small-scale laboratory experiment, I tested how brook trout and larval two-lined salamanders affected each other's prey consumption. Salamanders ate fewer prey with trout, but trout ate more prey in the presence of salamanders. The data suggest that as predators that often coexist with fish in streams, salamanders can influence invertebrate prey communities both directly and through density- and trait-mediated interactions.

Although trout had a clear impact on salamander density and activity, they had little impact on macroinvertebrates. Temporal and spatial changes in the invertebrate assemblage suggest that other factors are more relevant in this system at a large spatial scale.

CHAPTER 1

INTRODUCTION

A basic goal of ecology is to understand patterns of species distributions and abundance and to investigate relevant processes. Predation is one such process that can have important impacts on patterns of species abundance in natural systems. More specifically, important mechanisms such as interactions among multiple predators (Sih et al. 1998), indirect effects (Wootton 1994) and spatial scale (Wiens 1989, Levin 1992) can influence observed effects of predators on prey. Despite the benefits of decades of inquiry, the above topics remain sources of fruitful research.

The impact of predators on their prey has been a particularly dominant topic in stream ecology in recent decades. Some studies show the strong impact of predators in stream systems (Power 1992, Sih et al. 1992, Forrester 1994, Huryh 1998), yet many others show little or no predator impact (Allan 1982, Reice and Edwards 1986, Lancaster et al. 1991). Thus, it has been a central goal of stream ecologists in recent years to understand the underlying causes of variability in predator impacts on prey assemblages. Numerous studies have addressed the ambiguity of predator impacts in streams, identifying the potential importance of

methodological artifacts (Cooper et al. 1990), substrate heterogeneity (Ware 1972), prey size (McIntosh et al. 2002), indirect effects (Harvey 1993), prey behavior (Forrester 1994), predator foraging behavior (Dahl and Greenberg 1996), and spatial scale (Englund and Olsson 1996). A series of published models (Cooper et al. 1990, Sih and Wooster 1994, Englund 1997) addresses the effects of predators, ultimately stressing the importance of prey movement, prey behavior, and spatial scale. Each model builds on the previous models, increasing in complexity to improve our understanding of the effects of predators in streams.

In their seminal paper, Cooper et al. (1990) established a now standard metric for evaluating the impact of predators on the benthic density of prey as $PI = \ln(n_c/n_p)$, where n_c is the density of prey in predator-free or control patches and n_p is prey density in cages with predators. Predator impact (PI) is positive when $n_p < n_c$, negative when $n_p > n_c$, and zero when there is no predator effect on prey. Integrating their PI metric with a literature review, empirical data, and a conceptual model, Cooper et al. (1990) illustrated the strong effect of prey movement rate on PI.

In their literature review, Cooper et al (1990) showed that enclosure mesh size and invertebrate colonization drift rates explained differences in results among previously published studies. In relatively small-scale enclosure/exclosure experiments, cage mesh size (a measure of potential prey immigration and emigration) was negatively related to PI, suggesting

that PI was high in experiments using small mesh that restricted prey immigration. In five larger-scale (pool or stream section) manipulations, prey drift rates were one to two orders of magnitude lower in studies showing significant predator effect than studies showing no predator effect.

Cooper et al. (1990) also directly tested the effect of mesh size on impacts of predation in a series of experiments and a field study. Stoneflies reduced the density of *Baetis* (Ephemeroptera) in cages (10 x 10 x 10 cm) with small mesh but did not in cages with large mesh that allowed immigration and emigration. Mesh size did not affect chironomids (Diptera) in this experiment, probably because they are small enough to pass through both mesh sizes. Similarly, field data relating trout presence to prey drift and PI in 11 trout and 11 troutless pools showed a negative relationship between invertebrate turnover rate (number of invertebrates drifting out of pools per day divided by the number of invertebrates in the pools) and PI. These empirical and observational data further support the importance of prey exchange rates on PI.

The model presented by Cooper et al. (1990) illustrates the predicted response of prey density to prey movement and predator consumption. Their model suggests that at equilibrium ($dn_p/dt = 0$),

$$PI = \ln \left[\frac{(m + q)}{m} \right],$$

where m is the area-specific migration rate and q is the predation rate per prey (notation follows Englund 1997). Model simulation at varying levels of predation and prey exchange rates highlights that while the level of predation (q) impacts the observed PI (i.e., $\ln(n_c/n_p)$), prey exchange rate can have an overwhelming influence on PI (Figure 1-1).

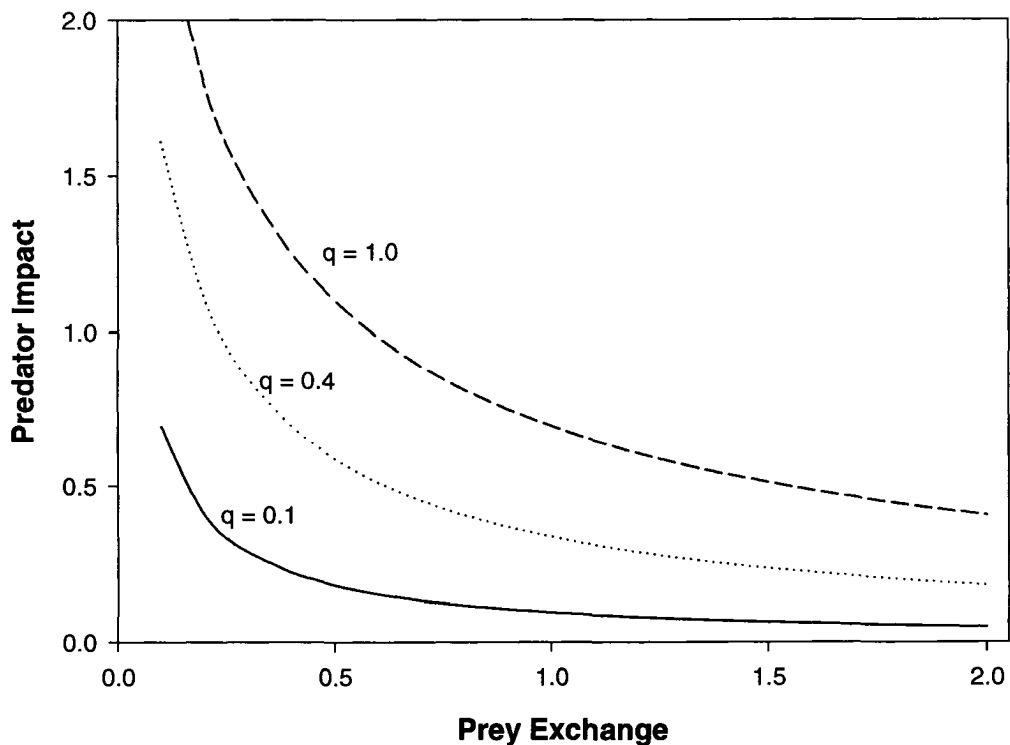


Figure 1-1: Model of predator impact as a function of prey exchange and predation rate (q). Modified from Cooper et al. 1990.

The literature review, empirical data, and model in Cooper et al. (1990) show strong support for the influence of prey exchange rates on predator impacts in stream predator manipulations; however, the model does not consider the effects of prey behavioral responses to predators.

Prey behaviorally respond to predators in numerous ways to reduce the probability of capture. Of particular importance to measuring predator impacts is the tendency of prey to increase (Peckarsky 1980, Kohler and McPeck 1989, Sih et al. 1992, McIntosh et al. 2002) or decrease (Bechara et al. 1993, McIntosh et al. 2002) their emigration rate in response to predators. Sih and Wooster (1994) modified the model above, allowing for differing rates of emigration from predator (m_p) and non-predator (m_c) patches to vary independently, such that

$$PI = \ln \left[\frac{(m_p + q)}{m_c} \right]$$

Model simulations showed that this modification could have strong effects on observed PI. For example, if prey attempt to avoid predation by leaving predator-occupied patches ($m_p > m_c$), PI will be enhanced (positive), regardless of the relative predator consumption rate (Figure 1-2). Perhaps more importantly, at all but very low exchange rates, if prey attempt to avoid predation by hiding in the substrate ($m_p < m_c$), PI will be negative even if predators consume a non-trivial proportion of prey. In the Sih and Wooster (1994) model, like the Cooper et al. (1990) model, PI decreases with increasing prey exchange; however, Sih and Wooster (1994) suggest that when migration from predator patches increases at a greater relative rate than migration from predator-free patches ($m_p \gg m_c$), PI can increase with prey exchange.

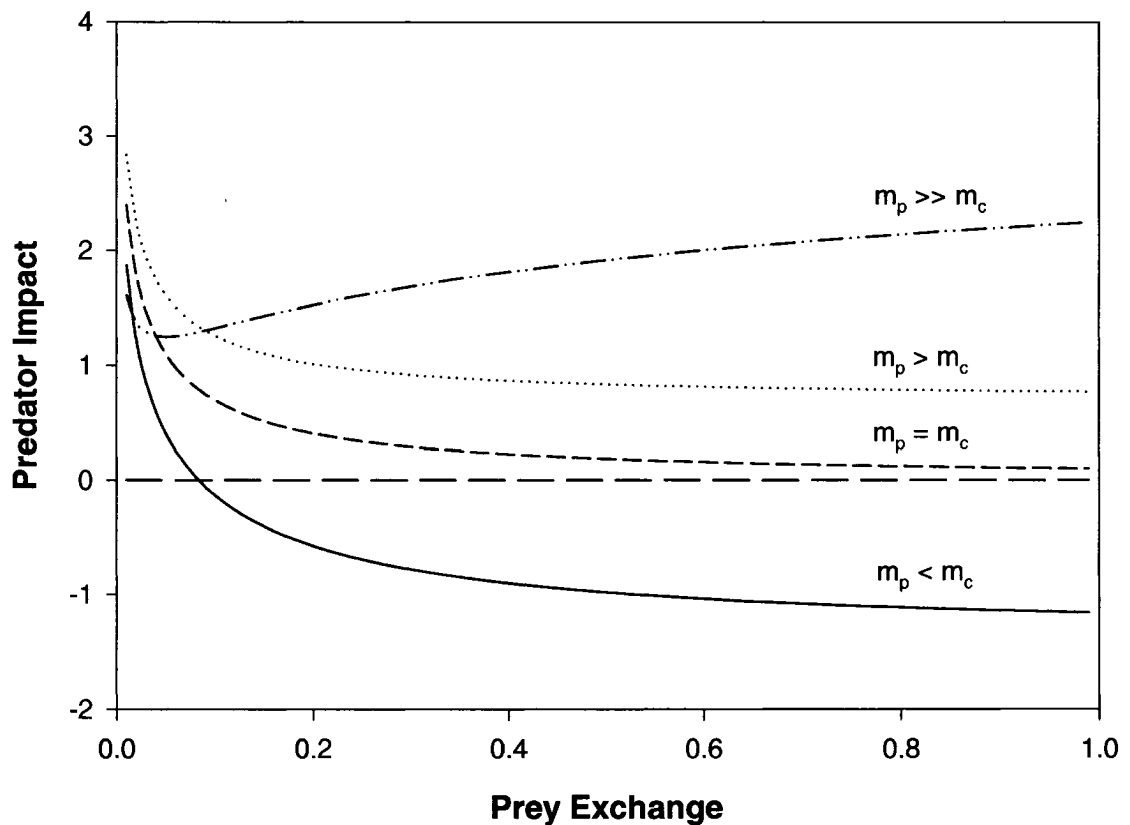


Figure 1-2: Model of predator impact as a function of prey exchange and relative rates of prey movement in predator-free (m_c) and predator occupied (m_p) habitats. Modified from Sih and Wooster (1994).

A number of studies support the Sih and Wooster (1994) model, illustrating the potentially strong impact of prey emigration behavior on PI. For example, drift and benthic density data from a study in 6-m long experimental streams showed decreased density of prey with greater behavioral drift responses to trout relative to taxa that did not increase emigration (Bechara et al. 1993, as analyzed by Wooster et al. 1997). Similarly, in 35-m-long field enclosures, prey density appeared to be more

related to prey emigration behavior than trout consumption (Forrester 1994).

It is clear that prey movement can have an important effect on the impacts of predator manipulations on prey populations in streams. The Cooper et al. (1990) model shows the strong impact of overall prey exchange on density, and Sih and Wooster (1994) underscore the importance of prey antipredator behavior. However, the 3rd model in the series deemphasizes the influence of behavioral drift at large, realistic spatial scales (Englund 1997). Rather than modeling PI at equilibrium ($dn/dt = 0$), Englund (1997) analyzed PI as a function of area and time (t), such that:

$$PI(t) = \ln \left[\frac{m_p - (m_p - m_c + q)e^{-(m_c - q)t}}{m_c - q} \right]$$

The model suggests that at small spatial scales, prey movement can have large but variable impacts that can override predation rates (Figure 1-3). Like the predictions made by the Sih and Wooster (1994) model, if emigration from predator patches is greater than non-predator patches ($m_p = 0.4, 0.8$), predator impacts can be large, though the influence of prey movement will decrease with increasing scale. If prey emigration from predator patches is small relative to predator-free patches ($m_p = 0.05$), predator impacts tend to be small but will increase with spatial scale.

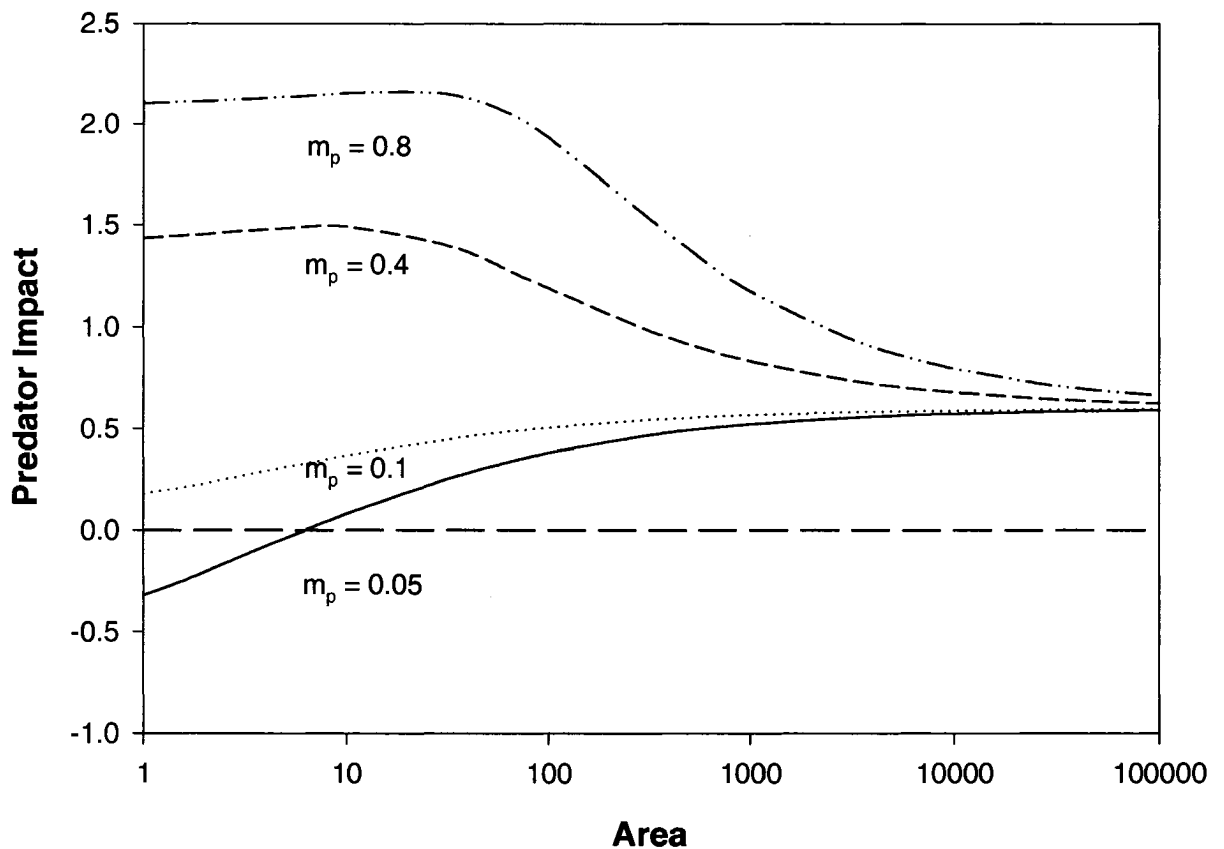


Figure 1-3: Model of predator impact as a function of area and migration rate from predator-occupied patches (m_p). Migration from predator-free patches (m_c) = 0.1 and time (t) = 30 units. Modified from Englund (1997).

However, in Englund's (1997) model, $m = m_u/A^{1/2}$ ($m_p = m_{up}/A^{1/2}$; $m_c = m_{uc}/A^{1/2}$), where m_u is the migration rate per unit area and A is area. If A is infinitely large, m_c and m_p approach zero, and the predator impact equation reduces to $PI = qt$. Thus, this model suggests that at large scales, the impacts of predator manipulation depend solely on predation rate and time (Figure 3).

Data from a relatively small-scale experiment (1 m² enclosures) support the above model by comparing prey migration rate with local PI

and an estimate of global (large-scale) PI (Englund and Olsson 1996). Englund and Olsson (1996) empirically measured local PI from the cage experiment and per capita migration rate per prey taxa as the ratio of relative drift abundance to relative benthic abundance. They indirectly estimated the global PI from sculpin (*Cottus gobio*) predation rate (ratio of relative abundance in sculpin diet to relative benthic abundance). They suggest that global PI should equal predation rate because as spatial scale increases, per capita migration rates become insignificant (above model). As predicted by the model, local PI was negatively related to per capita migration rate ($r = -0.68$); prey with higher drift rates showed lower PI in the small scale predation experiment. However, global PI (predation rate) was positively related to per capita migration rate ($r = 0.75$); prey with high drift rates were abundant in sculpin diets, perhaps because movement results in greater encounters with predators. Englund and Olsson's (1996) data support the Englund (1997) model and question the interpretation of small-scale experiments to natural systems. Interestingly, prey migration strongly influenced predator impact in a relatively large-scale predator manipulation experiment (35-m-long enclosures; Forrester 1994), thus larger-scale whole-stream manipulations may be necessary to decouple the interaction between benthic prey density and prey migration.

The above models (Cooper et al. 1990, Sih and Wooster 1994, Englund 1997) underscore the importance of prey exchange rates, prey antipredator behavior, and spatial scale on predator impacts in streams. Similarly, recent reviews of predator impacts on streams note the need for multi-scale comparisons of impacts of multiple predator types in the same system, simultaneous measurement of prey exchange and benthic prey density, and an understanding of mechanistic behaviors that underlie observed patterns (Wooster et al. 1997, Cooper et al. 1998). The above models have addressed these topics, yet their relevance to natural systems remains unclear. To identify patterns in prey activity and density in the presence and absence of brook trout (*Salvelinus fontinalis*) at a relatively large spatial and temporal scale, I conducted a field experiment in the White Mountain National Forest in New Hampshire. The field study included 9 streams: 3 with brook trout, 3 without fish, and 3 without fish to which I added brook trout (Figure 1-4).

In the White Mountain National Forest, brook trout are the most abundant and often only fish in low-order streams. Trout can affect macroinvertebrate activity (Huryn and Chivers 1999), benthic density (Bechara et al. 1992), and drift density (McIntosh and Peckarsky 1999) and periodicity (McIntosh and Peckarsky 1996, McIntosh et al. 2002). Similarly, predatory fish have a strong effect on larval salamander abundance, habitat use (Barr and Babbitt 2002), and surface activity (Petranka 1984).

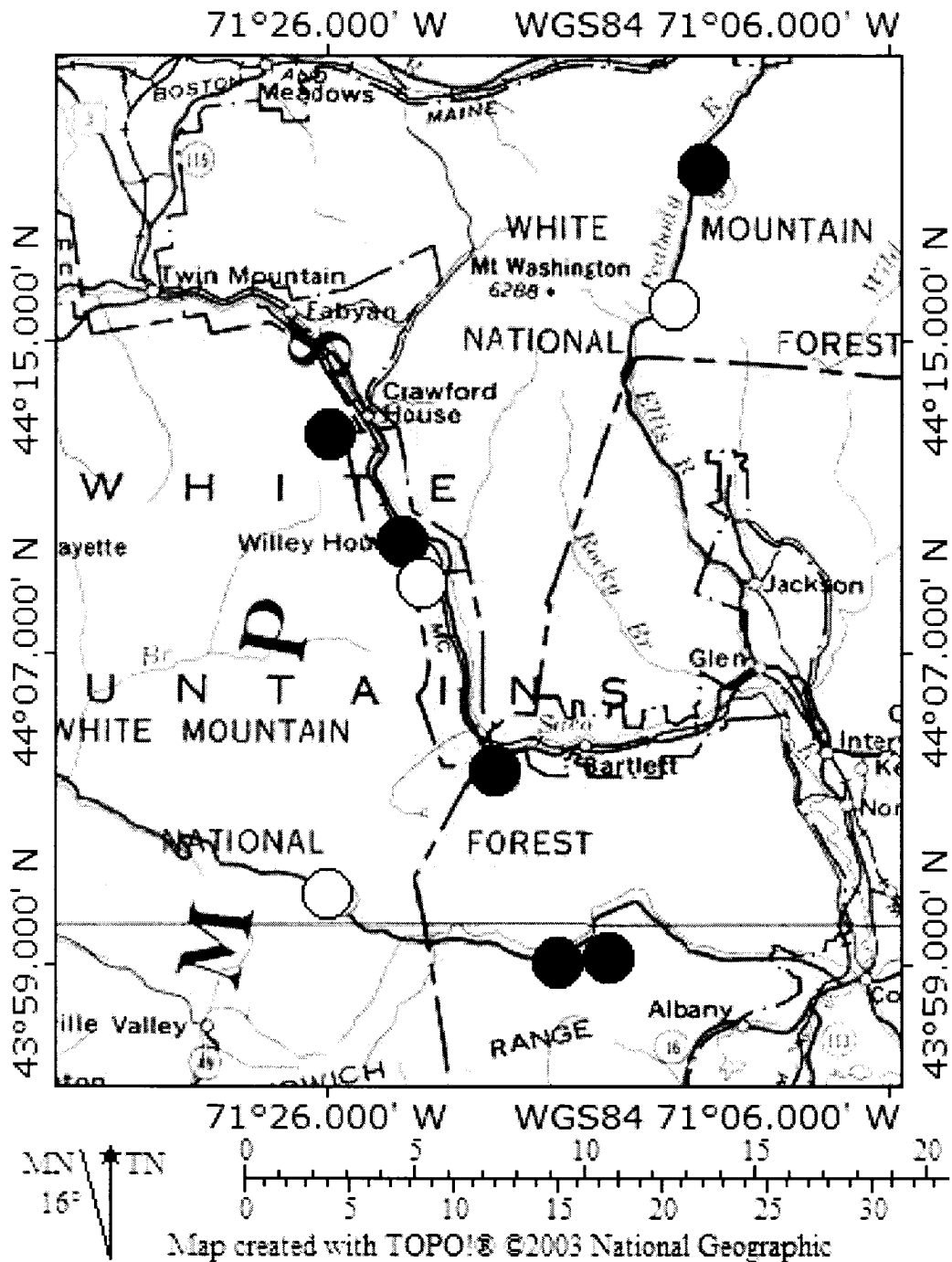


Figure 1-4: Map of streams sampled for the large-scale field experiment. Ledge (fishless), Twin (trout), and Steam Mill (addition) brooks flow into the Swift River. Stony (addition), Bemis (fishless), and Avalanche (trout) brooks flow into the Saco River. Crawford Brook (addition; above the Crawford) flows into the Ammonoosuc and Thompson (fishless) and Imp (trout) brooks flow into the Peabody River.

Brook trout occupy the entire elevational reach of some streams, yet they are absent above most waterfalls and cascades that block upstream movement in low-order streams (Barr, unpubl. data). Where trout are absent above waterfalls in the White Mountains, larval salamanders appear to be a dominant predator. In the absence of brook trout, larval two-lined salamanders (*Eurycea bislineata*) can be very abundant (up to 27 per 0.5-m²; Barr and Babbitt 2002), thus larval salamanders may have an important impact on invertebrate abundance and activity. In the presence of trout the abundance of two-lined salamander larvae is greatly reduced (< 4.7 per 0.5-m², Barr and Babbitt 2002). Despite their abundance in streams throughout the Appalachian Mountains (Beachy 1994, Barr and Babbitt 2002), the roles of larval plethodontid salamanders as predators and prey in streams remain understudied.

In the context of the above models, the abundance of larval salamanders in eastern stream systems and their spatial overlap with trout highlights the potential importance of interactions between trout and salamanders. The presence of multiple predators in natural systems is more common than not, and their impacts on prey can be complex (Sih et al. 1998). An increasing number of studies include multiple predators and investigate the nature and effect of interactions among them (Huang and Sih 1991b, Bechara et al. 1993, Diehl et al. 2000). For example, the

many studies of interactions among predatory fish, predatory stoneflies, and their shared prey show the complexity and variability of predator-prey interactions. Integral to understanding the impact of stoneflies and fish on invertebrate prey is an understanding of stonefly behavior and responses of prey to stonefly and fish foraging. Stoneflies behaviorally respond to fish predators by altering foraging activity and preferred substrate (Feltmate et al. 1986, Soluk and Collins 1988b), resulting in decreased prey capture by stoneflies (Soluk and Collins 1988c, 1988a). Similarly, many prey behaviorally avoid foraging stoneflies. For example, mayflies reduce movement and increase drift to reduce the risk of predation by stoneflies (McIntosh et al. 1999). Such behavioral responses can have important consequences such as lower size at emergence and lower egg biomass (Peckarsky et al. 1993, Peckarsky and McIntosh 1998). Similarly, mayflies commonly respond to fish by altering drift activity (McIntosh et al. 1999) and feeding rates, resulting in decreased size at emergence (Peckarsky and McIntosh 1998). Because mayflies and stoneflies respond to their predators, the presence of stoneflies modifies interactions between fish and their prey. For example, stoneflies facilitate prey capture for sculpin and trout (Soluk and Collins 1988c, Soluk 1993, Soluk and Richardson 1997). Identifying such interaction modifications is essential to understanding the effects of predators in manipulated systems.

Much like the interactions involving stoneflies and their predators and shared prey, the importance of larval salamanders as predators and prey in streams may be strongly related to behavior. Furthermore, the potential importance of behavioral effects and the presence of multiple predator and prey species suggest that indirect effects (behaviorally- and density-mediated) are particularly relevant. Due to the potential for indirect effects and the difference in trout and salamander foraging strategies, the effectiveness of invertebrate antipredator behavior should depend on trout presence. Avoidance strategies that are adaptive in the presence of larval salamanders may be ineffective in the presence of trout due to fish-induced changes in salamander behavior or fish predation. Such differences in predation pressure may ultimately affect invertebrate assemblage structure.

The objective of my large-scale manipulation of trout presence was to identify patterns in prey activity and density at a relatively large spatial and temporal scale. Chapter 2 focuses on macroinvertebrates as the prey taxa. By measuring invertebrate benthic and drift densities and trout predation rates on invertebrates, I measured differences in the invertebrate drifting and benthic assemblages among streams with and without trout, measured the short-term response of invertebrate drift behavior to trout addition, and tested the relevance of the 3 PI models at a realistic spatial scale. Chapter 3 focuses on larval two-lined salamanders

as prey and predators. By measuring the density and activity of salamanders in the same large-scale field experiment, I tested the behavioral and density responses of two-lined salamanders to trout presence. In a small-scale experiment, I also directly tested the effects of salamander and trout presence on each others' prey capture (and hence their impacts on benthic macroinvertebrates).

CHAPTER 2

THE RESPONSE OF STREAM MACROINVERTEBRATES TO A LARGE-SCALE MANIPULATION OF TROUT PRESENCE

Introduction

In recent decades, the impact of predators on their prey has been a particularly dominant and problematic topic in stream ecology. Some studies show the strong impact of predators in stream systems (Power 1992, Sih et al. 1992, Forrester 1994, Hury 1998), yet others show little or no predator impact (Allan 1982, Reice and Edwards 1986, Lancaster et al. 1991). Thus it has been a central goal of stream ecologists in recent years to understand the variability in predator impacts on prey assemblages. Numerous studies have addressed the ambiguity of predator impacts in streams, identifying the potential importance of methodological artifacts (Cooper et al. 1990), substrate heterogeneity (Ware 1972), prey size (McIntosh et al. 2002), indirect effects (Harvey 1993), prey behavior (Forrester 1994), predator foraging behavior (Dahl and Greenberg 1996), and spatial scale (Englund and Olsson 1996). A series of published models with supporting empirical evidence (Cooper et al. 1990, Sih and Wooster 1994, Englund 1997) highlight the particular importance of prey drift, anti-

predator behavior, and spatial scale on measurement of the effects of predators in streams.

The down-stream drift of macroinvertebrates is central to many studies on their interactions with predators. Although other factors clearly influence invertebrate drift (Kohler 1985, Siler et al. 2001, Malmqvist 2002), evidence indicates the strong influence of predation on drift behavior. For example, invertebrates commonly drift downstream to avoid benthic predators (e.g., stonefly nymphs) but will reduce drift rates, particularly during the day, in the presence of drift-feeding predators such as salmonid fish. Invertebrates also appear able to “fine tune” drift behavior according to a predator’s foraging activity (Huhta et al. 1999). Relatively large invertebrates that are most susceptible to fish predation often restrict their drift activity to nighttime when visually-feeding fish are less effective predators, whereas smaller, less vulnerable, invertebrates show little or no periodicity (Allan 1978, Malmqvist and Sjöström 1987, Tikkanen et al. 1994).

Despite the links between drift and predation, invertebrate drift is a confounding factor in many studies rather than an important metric. Studies of predation in streams using small enclosures with fine mesh prohibit movement of predators and prey into and out of enclosures. These “feeding experiments” often show a clear impact of predators on prey density (Cooper et al. 1990). As studies incorporate more realism by

using larger mesh to allow movement of prey into and out of enclosures, results can be quite different, showing that prey movement can swamp the direct effects of consumption on prey density (Cooper et al. 1990). Because prey may respond to the presence of predators by increasing or decreasing drift rates, small-scale studies can reflect predator impacts on prey behavioral drift rather than direct consumption (Forrester 1994, Sih and Wooster 1994, Wooster et al. 1997).

The link between small-scale responses of invertebrates and the impacts of predators on prey density at large, realistic spatial-scales is unclear. Even in relatively large field enclosures, prey density appears to be more related to prey behavior than trout consumption (35 m long, full stream width; Forrester 1994). However, as the size of an experimental unit increases, drift rates remain constant and the population in the benthos increases, thus per capita drift rates become relatively low (and approach zero; Englund 1997). Therefore, studies conducted at large spatial scales should reflect the impacts of trout predation, and studies conducted at small spatial scales should reflect prey behavior.

I conducted a large-scale manipulation to determine the effects of brook trout presence on patterns of invertebrate drift activity and benthic density. My objective was to identify patterns in invertebrate benthic and drift density in the presence and absence of brook trout (*Salvelinus fontinalis*) at a relatively large spatial and temporal scale. I hypothesized

that in all streams, invertebrate drift would show an increase in density at dusk and night but that the composition of drifting invertebrates would be different, particularly during the day, in streams with and without trout. Based on the predictions of Englund's (1997) model, I hypothesized that if drift rates differed among streams with and without trout, they would not be predictive of benthic density; differences among streams at a large spatial scale should be more closely related to predation rates than prey drift behavior.

Methods

I conducted this study in 1st and 2nd order streams in the White Mountain National Forest, a 300,000 ha National Forest in northern New Hampshire and western Maine. Within the National Forest, elevation generally ranges from 300 to 1200 m with some peaks above 1500 m. Streams in the White Mountains are cold, clear, and low in nutrients and productivity (Hornbeck and Leak 1992). Allochthonous detritus dominates production in low order streams (Fisher and Likens 1973, Hall et al. 2001).

I included 9 streams in the large-scale field experiment: 3 with brook trout (trout streams), 3 without fish (fishless streams), and 3 without fish to which I added brook trout (addition streams). Of the fishless streams I located above waterfalls (19 with similar physiognomy), I used 6 in the experiment to form 3 spatial blocks, such that 2 fishless streams were

relatively close to each other and were located near a similar stream with fish. Within each block, I randomly chose the fishless stream that received trout.

In trout and addition streams, I estimated fish density, using Zippin's (1958) equations, in a 100 m reach using a three-pass removal method with a backpack electroshocker. In each addition stream, I captured brook trout from below the waterfall and added them to an approximately 500 m reach above. This resulted in the relocation of 151 brook trout to a fishless reach in Crawford Brook (0.9 m², 30-240 mm total length), 103 in Stony Brook (0.3 m², 40-184 mm), and 149 in Steam Mill Brook (0.6 m², 45-174 mm). Immediately following capture and enumeration, I packaged fish individually in plastic bags and transported them with backpacks. Trout were not artificially restricted to their new stream reaches, but nearby waterfalls likely limited upstream movement. Sampling in 2003 showed that trout reproduced following relocation and maintained or increased their density.

Prior to trout translocation in 2002, I sampled invertebrate benthic density (10-14 July) and drift (9-19 July) in all 9 streams. I added brook trout to the 3 addition streams from 29 July to 1 August 2002. Following trout translocation in 2002, I sampled invertebrate drift (2-15 August) in all 9 streams. I also sampled invertebrate benthic density (July 8-15) and drift (July 7-27) in all nine streams in 2003. Therefore, with this sampling regime, I

collected invertebrate benthic density data before and 1 yr following trout translocation and drift density data before, shortly following, and 1 yr following trout translocation. For each sample period, I sampled streams randomly within spatial blocks, but sampled the blocks sequentially, always sampling the Crawford block first and the Kancamagus block last. When measuring drift immediately following trout addition, the 3 addition streams were sampled first because I sampled each on the day following trout addition.

To measure invertebrate drift density, I placed 1 drift net (31 x 31 x 100 cm, w x h x l; 200 μ m Nitex mesh; Aquatic Research Instruments, Hope, Idaho) at the outlet of each of 2 pools and riffles. I placed nets at the outlets of pools and riffles to capture the movement of individuals leaving these habitat units rather than to capture smaller-scale movements within units. I randomly chose the order of pools and riffles along the stream, yet the actual pool and riffle locations were chosen haphazardly because I placed nets: at least 2 pools and riffles or 30 m from each other, where there was measurable flow rate (with Global Water FP-1 flow meter, Gold River, California), and where I was able to insert metal stakes to anchor the nets. I collected the contents of each net every 2 h from approximately 3 h before to 3 h after sunset and preserved them in 70% ethyl alcohol. I chose sample times to estimate day (from 3 to 1 h before

sunset), dusk (from 1 h before to 1 h after sunset), and night (from 1 to 3 h after sunset) drift rates. I did not measure drift within 4 d of a full moon.

I sampled benthic invertebrates using a vacuum sampler modeled after Brown et al. (1987). The samplers were constructed with 45 cm (inside diameter) plastic culvert pipe. To one end of the pipe, I attached a foam tube to which I glued a doughnut-shaped piece of 10 cm thick foam. Additional pieces of foam were used during sampling to fill gaps between the sampler and substrate. The inside diameter of the foam ring was approximately 17.3 cm, resulting in a sample area of 0.23 m². A 12 V battery-powered marine utility pump (Teel 1P580E) pumped water at approximately 19 L min⁻¹ from inside the sampler through a PVC chamber (15 cm diameter, 40 cm long) containing a 200 µm Nitex mesh bag and back into the sampler. The mesh bag removed debris and invertebrates before water passed through the pump to avoid damaging invertebrates. In each stream, I collected one randomly placed sample from each of 10 consecutive pools and riffles. To control for effects of substrate, I only collected samples in areas dominated by pebbles (16-64 mm) and cobbles (64-256 mm) rather than finer and less abundant sand and gravel. For each sample, the pump was run for 10 min while the substrate was disturbed to a depth of 15 cm with a garden trowel. I preserved samples in 70% ethyl alcohol.

In the lab, I sifted all invertebrate samples into coarse and fine portions through a 1 mm sieve. I sorted invertebrates from debris at 10x (coarse) or 15x (fine) magnification and identified them to the family taxonomic level (Peckarsky et al. 1990, updated *Ameletus* family to Ameletidae from Siphonuridae) except Coleoptera (beetles), Lepidoptera (moths), Megaloptera (alder flies), Odonata (dragon- and damselflies), and individuals that were too small to accurately identify to the family level. I did not enumerate Hydrachnidia (mites), pupae, adults, or terrestrial invertebrates. Before sorting and identifying invertebrates in the fine portion of benthic samples, I separated them from most inorganic and organic debris by floating in a sugar solution (1.12 specific gravity; Anderson 1959). The sugar floating technique is effective because invertebrates are less dense than the sugar solution and most debris.

To estimate relative trout predation rates on macroinvertebrates, I sampled the stomach contents of approximately 30 brook trout (10 small, 10 medium, 10 large) in each stream with fish in 2002 (Avalanche, Twin, and Imp brooks) and 2003 (Avalanche, Twin, Imp, Stony, Steam Mill, and Crawford brooks). On each sample date, I collected fish in the morning (0800-1000) with a backpack electroshocker and flushed their stomach contents using the gastric lavage technique. I preserved gut contents in 70% ethyl alcohol and identified to the family taxonomic level when possible.

Statistical Analyses

I analyzed data in 3 main ways. I looked for: 1) univariate patterns in the drift and benthic densities of invertebrates, 2) multivariate patterns in the drifting and benthic invertebrates, and 3) patterns among drift density, benthic density, and trout predation rates as they relate to the 3 PI models (Cooper et al. 1990, Sih and Wooster 1994, Englund 1997). For univariate analyses, I used an Analysis of Variance (ANOVA) to test for differences in drift density among treatments in July and August 2002 and in July 2002 and 2003. In both cases, I had insufficient degrees of freedom to test the sample period, treatments, and time of day simultaneously, so for analyses that included time of day as a factor, I ran separate repeated measures ANOVAs for each sample period. I also used ANOVAs to test broad patterns in benthic densities among treatments and years. I used log transformed data in all univariate drift and benthic analyses.

For multivariate analyses of patterns in macroinvertebrate assemblages among streams, treatments, and between sample periods, I used Nonmetric Multidimensional Scaling (NMS; Kruskal 1964b, 1964a, Mather 1976). Nonmetric Multidimensional Scaling has no assumptions of multivariate normality, is robust to zero-values in the data matrix, and can yield the most accurate representation of underlying data structure (Minchin 1987, Clarke 1993, Peterson and McCune 2001). In the NMS analyses, I used the Sorensen distance measure, a random starting

configuration, and 400 iterations with my data using PC-ORD 5.01 (McCune and Mefford 1999). I ran a Monte Carlo test using 40 runs with randomized data to identify whether the axes identified with my data were stronger than expected by chance. Preliminary analyses were run with 6 axes, and I determined the number of axes in subsequent and final solutions using a scree plot and Monte Carlo results. I confirmed the stability of solutions using plots of stress (a measure of fit) versus iteration number (McCune and Grace 2002). I ran multiple analyses with random starting configurations to ensure consistent results. The analysis of benthic data was varimax rotated to more clearly represent the results graphically.

For NMS analyses, I combined the number of invertebrates counted for each taxon in the coarse and fine portions of samples, except in the orders Ephemeroptera, Plecoptera, and Trichoptera. Due to the very small sizes and difficulty of identifying to family, Plecoptera and Trichoptera counted in the fine portions of samples were combined into "small Plecoptera" and "small Trichoptera" categories, respectively. Due to the relative ease of identifying small Ephemeroptera to family and their abundance in some families (e.g., Baetidae), I created separate categories for the coarse and fine ("small") portions of samples. Due to rarity among and within streams, Peltoperlidae (Plecoptera) and Uenoidae (Trichoptera) were not included in analyses. Due to small size,

low abundance, and relative rarity, I did not include Copapoda and Ostracoda in analyses. Water striders (Gerridae, Hemiptera) were also captured but not included in analyses because they are surface-dwellers.

To reduce the dominance of abundant taxa in NMS analyses, I log transformed benthic and drift density data. Because the smallest nonzero values were orders of magnitude smaller than 1 (0.001 drift, 0.01 benthic), a standard $\log(x + 1)$ transformation would distort the difference between zero and other values (McCune and Grace 2002). Thus to transform drift density, I used the formula $b = \log(x + d) - c$, where b is transformed data, x is untransformed data, $c = \text{int}(\log(\min(x)))$, the $\text{int}(x)$ function drops digits after the decimal point to make x an integer, $\min(x)$ is the smallest nonzero value in the data set, and $d = \log^{-1}(c)$.

I analyzed how well my field results fit the predictions of 3 conceptual models of predator impacts on prey (Cooper et al. 1990, Sih and Wooster 1994, Englund 1997) by calculating and comparing indices of PI, the propensity of invertebrates to drift, the relative propensity of invertebrates to drift in trout and fishless streams, and trout predation rates for each taxon. I calculated the predator impact index as $PI = \ln(n_c/n_p)$, where n_c is the density of invertebrates in streams without trout (control) and n_p is the density of invertebrates in streams with trout (predator). Predator impact (PI) is positive when $n_c > n_p$ (predators reduce prey

density), negative when $n_p > n_c$, and zero when there is no predator effect on prey density. Because invertebrate densities differed between 2002 and 2003, irrespective of trout presence, I calculated PI using trout and fishless streams separately in 2002 and 2003, then took the mean for an average PI value. I calculated the propensity to drift for each taxon as the drift density divided by the benthic density. I also calculated this metric separately for trout and fishless streams. I calculated the relative propensity to drift as the propensity to drift in trout streams divided by the propensity to drift in fishless streams. I calculated trout predation rates for each taxon as the proportion of each taxon in the stomachs of all trout in 2002 and 2003 divided by its mean benthic density. I used Spearman's rank correlations to measure the relationship between variables.

Results

Drift

I enumerated 45,869 invertebrates in the July 2002 drift samples, 27,525 invertebrates in the August 2002 samples, and 37,229 invertebrates in the July 2003 samples. Average drift density was $5.10 \pm 0.31 \text{ m}^{-3}$ (mean \pm 1SE) in July and $6.21 \pm 0.44 \text{ m}^{-3}$ August 2002 and $6.44 \pm 0.78 \text{ m}^{-3}$ in July 2003. For the 2002 samples, differences in total drift among treatments ($F_{2,12} = 0.587$, $p = 0.571$) and between sample periods ($F_{1,12} = 1.516$, $p = 0.242$) were not significant (Figure 2-1). Total drift density varied significantly by time of day in July ($F_{2,12} = 29.7$, $p < 0.001$; Figure 2-2 A) and August ($F_{2,12} =$

6.64, $p = 0.011$; Figure 2-2 B) but did not differ among treatments (July $F_{2,6} = 0.294$, $p = 0.755$; August $F_{2,6} = 0.341$, $p = 0.724$). Night drift was higher than day (Tukey: July $p = 0.010$, August $p = 0.035$); dusk samples were intermediate but not significantly different from day or night. Patterns were similar for comparisons between the July 2002 and 2003 drift samples. Differences in total drift among treatments ($F_{2,11} = 0.428$, $p = 0.662$) and between sample periods ($F_{1,11} = 1.337$, $p = 0.272$) were not significant (Figure 2-3), but drift density varied by time of day (2002 $F_{2,12} = 31.331$, $p < 0.001$; 2003 $F_{2,10} = 27.197$, $p < 0.001$; Figure 2-4). Drift was dominated ($> 15\%$) by Chironomidae (49.7%; Diptera) and Baetidae (29.4%; Ephemeroptera) larvae in July 2002, Chironomidae (39.9%), Baetidae (28.8%), and small Trichoptera (15.6%) larvae in August 2002, and Chironomidae (50.9%) in July 2003.

Total drift density was $5.36 \pm 0.31 \text{ m}^{-3}$ exiting pools and $5.95 \pm 0.45 \text{ m}^{-3}$ exiting riffles ($t_8 = -0.752$, $p = 0.474$). When preliminary ordination analyses were run using pool and riffle data as separate samples, distances in ordination space between pools and riffles for a given stream varied. However, results for analyses with pool and riffle data combined within each stream are presented because they show similar patterns and are less cluttered.

Uenoidae, Limnephilidae (Trichoptera), and Odonata nymphs were the only invertebrates I captured in benthic and drift samples that were

absent from drift net samples in streams containing trout. I only caught one each of Uenoids and Limnephilids in drift samples, thus their drift response to trout is unclear or irrelevant. Odonata were uncommon in drift (and benthic) samples, yet their absence from drift (and many benthic) samples from streams with fish suggests an important behavioral avoidance (and perhaps predatory effect) of trout by Odonata.

The NMS analysis of July and August 2002 log-transformed drift density data resulted in a 3-dimensional solution that explained 88.0% of the variance (R^2 Axis 1 = 0.12, Axis 2 = 0.43, Axis 3 = 0.32) between the distance in ordination space and distance in the original space. I ran 400 iterations in the final solution, resulting in a stable solution with a stress of 12.3. The Monte Carlo analysis showed a 0.02 probability of reaching a similar final stress with randomized data.

The ordination using log-transformed data illustrates the considerable variation among streams, irrespective of treatment, and is dominated by overall changes in invertebrate abundance from July to August and among the day, dusk, and night samples (Figure 2-5). Relatively strong correlations ($R^2 > 0.2$) of 15 invertebrate taxa in the analysis with Axis 2 show that the drift of most invertebrates changed from day to dusk to night in all streams (Table 2-1). Similarly, univariate plots clearly show that all taxa increased from day to night, except Rhyacophilidae (only in August when Rhyacophilidae were relatively

small), small Trichoptera, Simuliidae, Nymphomyiidae, and Megaloptera. Axis 3 separates the July and August samples, showing that Ameletidae, Heptageniidae, and Megaloptera nymphs decreased and small Baetidae, Rhyacophilidae, and small Trichoptera increased in the drift from July to August (Table 2-1).

Although I can identify no clear patterns related to the trout treatments in the NMS analysis of invertebrate drift, some univariate patterns in drift are clear upon investigation of data by taxon. For example, Ameletidae, Ephemerellidae, and Hydropsychidae drifted at night but not during the day in streams with fish; they did drift during the day in fishless streams but at a lower density than night. This is in contrast to other taxa that drifted at relatively low density during the day in both fish and fishless streams.

The NMS analysis of July 2002 and 2003 log-transformed drift density data resulted in a 3-dimensional solution that explained 90% of the variance (R^2 Axis 1 = 0.16, Axis 2 = 0.32, Axis 3 = 0.42) between the distance in ordination space and distance in the original space. I ran 400 iterations in the final solution, resulting in a stable solution with a stress of 11.3. The Monte Carlo analysis showed a 0.004 probability of reaching a similar final stress with randomized data.

The ordination using log-transformed data illustrates the considerable variation among streams, irrespective of treatment, and is

dominated by overall changes in invertebrate abundance among the day, dusk, and night samples and from 2002 to 2003 (Figure 2-6). Like the ordination of July and August 2002 data, the drift density of most taxa increased at night. The correlations ($r^2 > 0.2$) of 15 invertebrate taxa in the analysis with Axis 3 show that the drift of most invertebrates changed from day to dusk to night in all streams (Table 2-2). Similarly, univariate plots show that all taxa increased from day to night, except "other Diptera" and Megaloptera. Axis 1 roughly distinguishes the 2002 and 2003 samples, though the separation is less clear than in the July-August 2002 analysis. Taxon correlations with Axis 1 show that Ephemerellidae, small Siphonuridae, small Leptophlebiidae, small Plecoptera, Lepidostomatidae, small Trichoptera, Chironomidae, Simuliidae, and "other Diptera" increased in the drift from July 2002 to 2003 (Table 2-2). Like the comparisons of invertebrate drift among streams in July and August 2002, comparisons between 2002 and 2003 do not reflect differences related to the presence or addition of trout.

Benthic

I enumerated 40,245 invertebrates in 2002 and 107,088 invertebrates in the 2003 benthic samples. Average density was 232 ± 36 per 0.23 m^2 (mean \pm 1SE) in 2002 and 597 ± 111 per 0.23 m^2 in 2003 and varied considerably among streams. Density increased from 2002 to 2003 ($F_{1,12} = 16.01$, $p = 0.002$) but showed no clear patterns among treatments ($F_{2,12} =$

1.43, $p = 0.28$; Figure 2-7). Interestingly, the streams with the highest (Imp) and lowest (Avalanche) densities in 2002 both contained trout. Invertebrate density was 296.1 ± 49.9 per 0.23 m^2 in pools and 166.5 ± 23.6 per 0.23 m^2 in riffles in 2002 and 783.5 ± 151.9 per 0.23 m^2 in pools and 407.1 ± 83.2 per 0.23 m^2 in riffles in 2003. Benthic density was dominated by Chironomidae larvae in both years (72% in 2002, 74% in 2003).

The NMS analysis of July 2002 and 2003 log-transformed benthic density data was varimax-rotated and resulted in a 3-dimensional solution that explained 91.5% of the variance (R^2 axis 1 = 0.05, axis 2 = 0.55, axis 3 = 0.32) between the distance in ordination space and distance in the original space. I ran 400 iterations in the final solution, resulting in a stable solution with a stress of 7.63. The Monte Carlo analysis showed a 0.004 probability of reaching a similar final stress with randomized data.

The organization of streams in ordination space shows considerable variation among streams and is dominated by differences between 2002 and 2003 and differences among spatial blocks, irrespective of treatment (Figure 2-8). Correlations of 16 taxa with axis 2 and univariate plots show that Leptophlebiidae, small Ephemeroptera, small Plecoptera, small Trichoptera, Lepidostomatidae, Odontoceridae, and most Diptera increased in abundance from 2002 to 2003 (Table 2-3). No taxon was absent from all streams with trout or streams without fish.

Fish guts

I flushed a total of 3022 items from 269 brook trout (839 from 85 trout in 2002; 2183 from 184 trout in 2003) for an average of 11.2 per fish (9.9 in 2002; 11.9 in 2003). Stomach contents were dominated by Chironomidae larvae and terrestrial invertebrates (Figure 2-9) and included other aquatic invertebrate nymphs, small brook trout, a two-lined salamander, water striders, invertebrate egg masses, and parasites.

PI models

I found no clear patterns between the PI of each taxon and its propensity to drift ($r_s = -0.17$; Figure 2-10), relative (in fish vs. fishless streams) propensity to drift ($r_s = 0.21$; Figure 2-11), and trout predation rate ($r_s = -0.15$; Figure 2-12). However, the data do show that taxa with relatively high daytime drift rates tended to experience high trout predation ($r_s = 0.27$; Figure 2-13).

Discussion

Describing general patterns in the effects of predators on their prey in stream systems has been a difficult endeavor, particularly at large, realistic spatial-scales. The Cooper et al. (1990) and Sih and Wooster (1994) models suggest that drift rates and anti-predator behavior may affect prey density more than predator consumption. The Englund (1997) model shows that as the spatial scale of experimental arenas increases, per capita drift rates decrease, thus the impacts of predators on their prey should be directly due to predation rather than prey behavior. However, at the relatively large spatial and temporal scales used in this study, I did not find a clear and strong impact of trout on invertebrate drift or benthic density. Relative to temporal fluctuations and spatial differences in invertebrate benthic and drift density, the influence of trout on stream macroinvertebrates in New England mountain streams appears to be low.

Despite the poor relationship of invertebrate drift and benthic densities with trout presence, several patterns are evident, including the spatial and temporal patterns in benthic and drift densities, diel drift periodicity, and relationships of invertebrate drift with trout predation rates. The spatial pattern among streams and temporal relationships between samples seem to dominate patterns in benthic and drift densities of invertebrates. For example, the only differences in total invertebrate benthic density were between the 2002 and 2003 sample periods.

Likewise, differences in total drift density were only significant among sample periods and between day and nighttime. In multivariate analyses, the clearest differences are among sample periods and, for drift, the time of day. There was a clear change in the drifting invertebrate assemblages between my July and August sample periods. This appears to be largely related to phenological changes in the abundance of a few taxa (increased abundance of very small Trichoptera and Megaloptera, maturation of Rhyacophilidae to identifiable instars, and several Ephemeroptera).

For the benthic samples, differences among the spatial blocks seem as important as the time between sample periods. Streams closer in space appear to have more similar invertebrate assemblages. Such similarities may reflect habitat, forest composition, elevation, or geology. However, like the temporal patterns in both drift and benthic assemblages, the spatial patterns in benthic density are unrelated to the presence of fish. If trout affect the drift or benthic densities of invertebrates, most impacts appear to be masked by more influential spatial and temporal changes in assemblage composition.

Across all streams, one of the clearest patterns is the increase in drift density from day to nighttime samples. This diel drift periodicity is a well documented phenomenon (reviewed by Waters 1972, Brittain and Eikeland 1988) and is somewhat ubiquitous. Although many factors can

affect drift density, substantial evidence supports the influence of predatory fish on diel drift behavior. Because trout are visual predators, they feed mainly during daylight hours (Bisson 1978, Allan 1981), and the susceptibility of drifting macroinvertebrates to predation is much lower at night (McIntosh et al. 2002). Invertebrate drift is aperiodic in the absence of drift-feeding predators in only a few cases, such as island (Malmqvist 1988) and high-elevation streams (Turcotte and Harper 1982, Flecker 1992, Jacobsen and Bojsen 2002) that historically lacked drift-feeding predators.

Despite the theoretical and empirical links of drift to predation, my data show little evidence of invertebrates behaviorally responding to trout. All but a few taxa show similar patterns in fish and fishless streams. In contrast, some studies show remarkably adaptive fine-tuning of drift behavior (Huhta et al. 1999, McIntosh et al. 1999). For example, large *Baetis rhodani* mayfly nymphs adjust their drift according to fish and invertebrate predator foraging activity such that drift is aperiodic with an aperiodically foraging caddis larva but nocturnal with nocturnally foraging fish and stonefly nymphs (Huhta et al. 1999). McIntosh et al. (1999) piped additional fish odor into a trout stream, causing a decrease in large *Baetis* drift and an increase in small *Baetis* drift. The fine-tuning of *Baetis* nymphs to predator cues suggests that some invertebrates are well adapted for heterogeneous environments that may contain relatively safe, fish-free habitats within a background of fish-occupied streams.

Perhaps in the New England mountain stream systems used in this study, the likelihood of drifting into a fish stream limits the daytime drift of macroinvertebrates in fishless streams. Brook trout are rarely absent from 2nd order streams and occur throughout the entire reach of some streams where no barrier to movement exists. Even in fishless stream reaches, trout are likely present within close proximity down stream. Therefore, in the absence of chemical, visual, and hydrodynamic cues from fish, invertebrates cannot safely assume that drifting will lead to a fishless pool. The few studies that have estimated the total downstream drift distances over the aquatic life of an invertebrate suggest that amphipods (*Gammarus*) drift 1.5-km from hatching to first reproductive episode (180 days; Humphries and Ruxton 2003) and up to half of mayfly nymphs (*Baetis*) drift at least 2.1 km during the arctic summer (Hershey et al. 1993). Relatively few stream reaches are far from fish, thus relatively few invertebrates are predictably safe from fish predation and, on an evolutionary time-scale, prey in fishless streams are not naïve to fish. Perhaps “testing the waters” by drifting during the day is too dangerous.

Illustrating the dangerous nature of drifting with trout, invertebrate taxa with the highest propensity to drift were most common in the stomachs of trout. Among the 10 “taxa” (includes terrestrial invertebrates and small Trichoptera) that accounted for at least 2% of trout gut contents, 5 were among the 10 most abundant drifters (3 were not

quantified in drift samples: terrestrial invertebrates, Chironomidae pupae, and mites). The presence of the other 2 taxa, Lepidostomatidae and Odontoceridae caddisfly larvae, in trout stomachs and their absence (Odontoceridae) or rarity (Lepidostomatidae) in the drift suggests trout were feeding in part from the epibenthos.

Although taxa with a high propensity to drift are more common in trout stomachs, this high predation rate is not reflected in differences between fish and fishless streams. I did not find a clear relationship between predation rates and the PI index among taxa. Likewise, I found no other clear patterns among predation rates and drift behavior with benthic densities among streams. Because I found no strong impact of trout on the benthic or drift densities of macroinvertebrates, it should be of little surprise that I also did not identify clear patterns among the PI index and invertebrate drift rates, relative drift rates with and without fish, and predation rates.

Some empirical evidence suggests there should be relationships between benthic density and predation, drift, and drift behavior (Cooper et al. 1990, Sih and Wooster 1994, Englund 1997). However, at the large spatial and temporal scales used in this study, where many factors can affect invertebrate drift and benthic densities, the models seem to have little relevance. Indeed, the poor relationship between fish presence and the macroinvertebrate assemblage suggests there are more important

sources of mortality and recruitment that affect invertebrate abundance in these streams.

Stream macroinvertebrates are notoriously variable at multiple spatial scales (Allan and Russek 1985, Heino et al. 2004) and their presence and abundance in the benthos and drift depend on many factors. Although the 9 streams used in this study are from a relatively small region with broadly similar habitat, geology, and land use history, minor differences in such factors as well as finer-scale variation in stream habitat (proportions of pool, riffle, run, cascade; small-scale flow regime and substrate characteristics) and productivity may affect invertebrate assemblages. Habitat quality, measured using food availability (Kohler 1985) and predation pressure (Fairchild and Holomuzki 2005) can alter prey drift rates. Similarly, several studies show the importance of density-dependence in regulating invertebrate populations. Removing most alderfly eggs or nearly doubling egg density in stream reaches resulted in short term effects (Hildrew et al. 2004), perhaps due to colonization, emigration, and predation (Walton 1980). Therefore, even in the absence of a potentially important predator, trout, other factors limit the density of invertebrates.

Some sampling artifacts may have affected my ability to accurately measure the impacts of fish in this system. For example, I identified most invertebrates to the family taxonomic level. McPeck

(1990) illustrated that Odonata species within the genus *Enallagma* respond differently to fish, thus the effects of trout on stream invertebrates may be more clear at the genus or species level. However, due to the difficulty and time required to identify macroinvertebrates to species, this is unrealistic in many situations, particularly replicated studies conducted at large spatial-scales. Many studies support the use of Family-level identification for analyses of invertebrate assemblages, showing little benefit from genus or species-level identification (Waite et al. 2004). Similarly, Family-level analyses will result in fewer zeroes, an issue that plagues analysis of community data sets (McCune and Grace 2002).

Furthermore, perhaps this New England, forested system with coarse substrates and little in-stream primary production, is exactly where we should expect trout to have a minimal impact on their prey. The benthic substrates of streams in the White Mountains are coarse, with many large boulders and cobbles. Research suggests the impact of predatory fish on the benthic abundance and drift behavior of their prey is greater on substrates with fewer interstitial spaces for refuge (Williams and Moore 1982, Fairchild and Holomuzki 2005). Similarly, most northeastern streams in relatively undisturbed landscapes are exposed to little direct sunlight. Many of the studies reporting an impact of fish on invertebrates and algae are in systems with relatively open canopies where an important part of the invertebrate production is supported by periphytic algae

(Power 1990, McIntosh and Townsend 1996). In such systems, there can be a clear conflict between foraging and predator avoidance; the upper surfaces of the substrate are rich in food but dangerously exposed to predators. Density- and behaviorally-mediated impacts of trout can result in clear changes in invertebrate abundance and algal standing crop (McIntosh and Townsend 1996). In contrast, small streams with a closed canopy receive little sunlight and are supported mainly by litter inputs from the surrounding forest. Invertebrates can forage within the substrate and limit their exposure to trout predation.

The data from this large-scale field experiment suggest that trout have little impact on the behavior and density of stream macroinvertebrates in small, forested streams. Despite theoretical and empirical evidence to suggest that invertebrates alter their activity in the presence of trout, such patterns were not clear in this field experiment. Likewise, models and experiments suggest trout should reduce their prey's abundance at large scales due predation, yet they seem to have no impact in this field experiment. Such results lend support to concerns over the translation of small-scale results to the larger scale and more variable conditions experienced by organisms in natural systems. Further research at large spatial and temporal scales in other types of stream systems may help distinguish the conditions in which fish measurably affect macroinvertebrate behavior and density.

Table 2-1: Squared Pearson correlations (r^2) among taxa and ordination axes from the NMS ordination of invertebrate drift samples in July and August 2002. Cells are included if correlations are greater than 0.2. R^2 represents the proportion of variance between ordination and original space that is represented by each axis.

Axis:	1	2	3
R^2	0.12	0.43	0.32
Taxon	r^2	r^2	r^2
Baetidae		0.295	
Ameletidae		0.214	0.294
Ephemerellidae		0.485	
Heptageniidae		0.513	0.234
smBaetidae	0.288		0.276
smEphemerellidae		0.264	
smLeptophlebiidae		0.275	
Leuctridae		0.408	
Chloroperlidae		0.634	
Nemouridae		0.493	
Perlodidae		0.533	
smPlecoptera		0.352	
Philopotamidae		0.255	
Rhyacophilidae			0.227
Lepidostomatidae		0.239	
Polycentropodidae		0.364	
smTrichoptera			0.877
Simuliidae	0.393		
Tipulidae		0.508	
Nymphomyiidae	0.509		
Megaloptera			0.419

Table 2-2: Squared Pearson correlations (r^2) among taxa and ordination axes from the NMS ordination of invertebrate drift samples in July 2002 and 2003. Cells are included if correlations are greater than 0.2. R^2 represents the proportion of variance between ordination and original space that is represented by each axis.

Axis:	1	2	3
R^2	0.160	0.316	0.419
Taxon	r^2	r^2	r^2
Baetidae		0.222	0.396
Ameletidae		0.305	
Ephemerellidae	0.234		0.453
Heptageniidae		0.4	0.368
smBaetidae		0.371	0.208
smAmeletidae	0.232		
smHeptageniidae		0.489	
smLeptophlebiidae	0.2		
Leuctridae			0.577
Chloroperlidae			0.647
Nemouridae		0.428	0.485
Perlodidae		0.234	0.481
smPlecoptera	0.319	0.281	0.383
Philopotamidae			0.303
Rhyacophilidae			0.357
Hydropsychidae			0.218
Lepidostomatidae	0.258		
Polycentropodidae		0.198	0.279
smTrichoptera	0.52	0.205	
Chironomidae	0.391		0.364
Simuliidae	0.471		
Tipulidae		0.231	0.445
Nymphomyiidae		0.229	
otherDiptera	0.353		
Megaloptera		0.465	

Table 2-3: Squared Pearson correlations (r^2) among taxa and ordination axes from the NMS ordination of invertebrate benthic samples in July 2002 and 2003. Cells are included if correlations are greater than 0.2. R^2 represents the proportion of variance between ordination and original space that is represented by each axis.

Axis:	1	2	3
R ²	0.05	0.55	0.32
Taxon	r²	r²	r²
Ephemerellidae	0.397		
Leptophlebiidae		0.362	
smBaetidae		0.319	0.278
smAmeletidae	0.268	0.21	
smEphemerellidae		0.692	
smHeptageniidae		0.216	0.37
smLeptophlebiidae		0.395	
Leuctridae	0.451		0.275
Chloroperlidae	0.199		
Nemouridae	0.384		0.341
Perlodidae	0.28		
smPlecoptera		0.552	
Philopotamidae	0.33		
Rhyacophilidae	0.589		
Hydropsychidae			
Lepidostomatidae	0.201	0.203	0.456
Limnephilidae	0.334		
Odontoceridae		0.374	
smTrichoptera		0.351	
Chironomidae		0.649	
Ceratopogonidae		0.692	
Simuliidae		0.446	
Tipulidae		0.608	
Nymphoyiidae			0.691
otherDiptera		0.463	0.277
Coleoptera		0.432	
Odonata			
Megaloptera	0.537		0.395

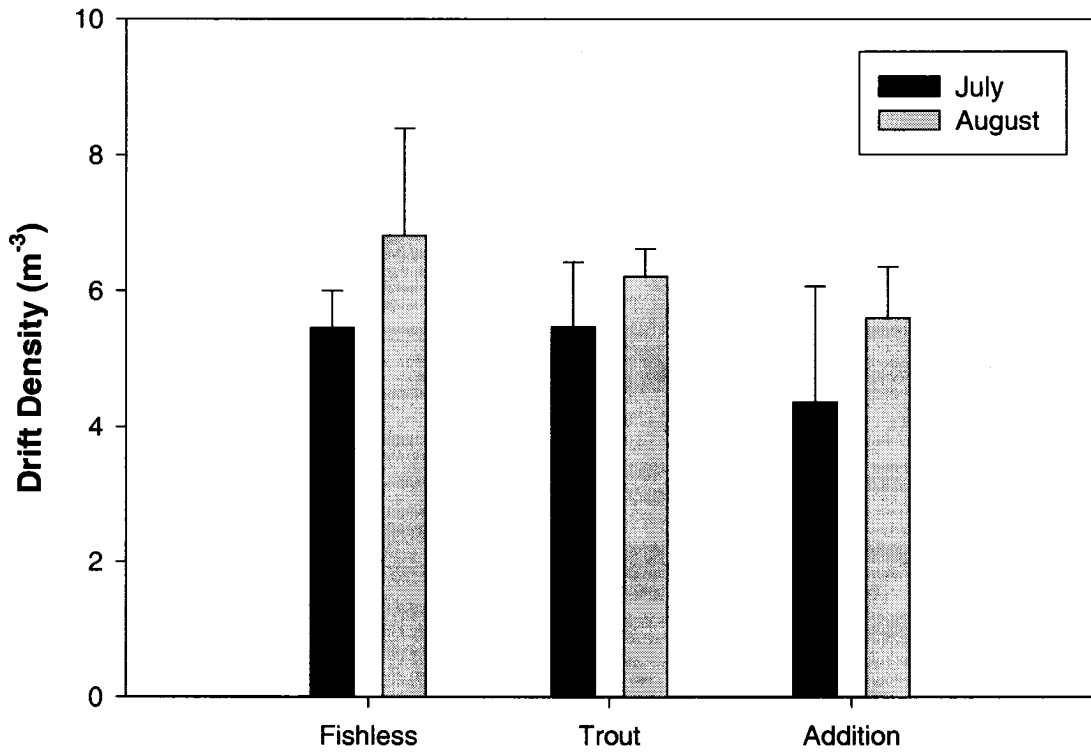


Figure 2-1. Mean (+ 1SE) invertebrate drift density among treatments in the July and August 2002 samples in: fishless streams containing no fish and trout streams containing brook trout throughout the experiment, and addition streams that were fishless until I added brook trout following the July 2002 samples. N = 3.

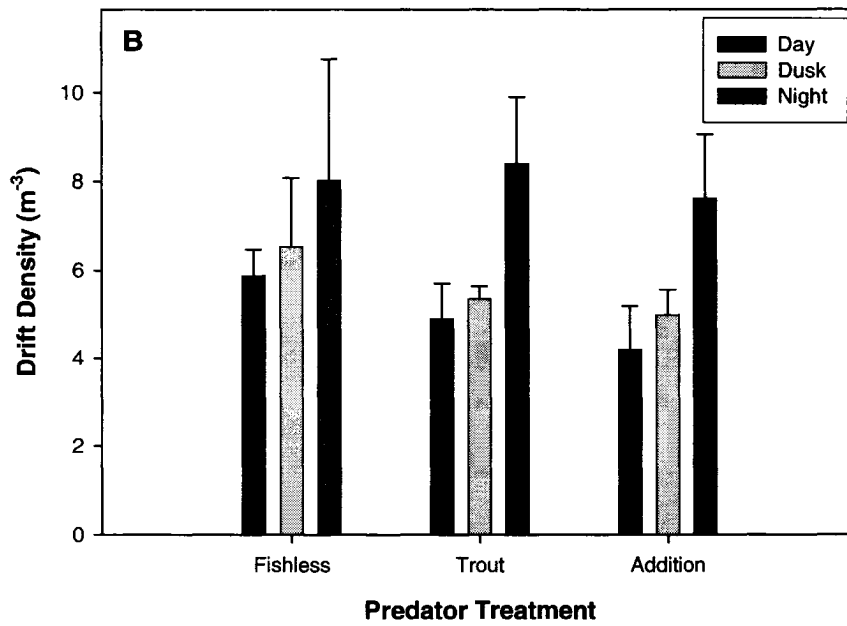
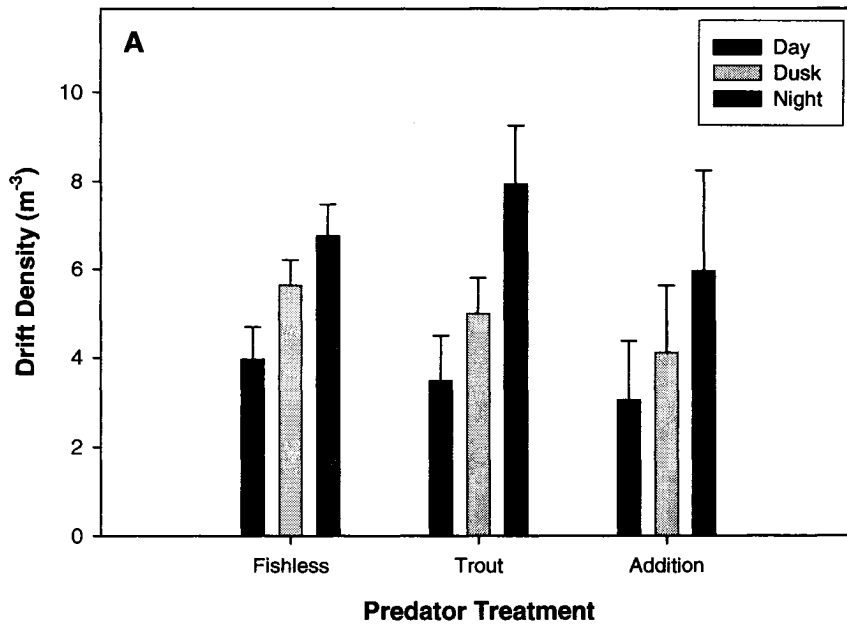


Figure 2-2. Drift density (+ 1SE) among treatments during day (~17-1900), dusk (~19-2100), and night (~21-2300) samples in A) July and B) August. Fishless streams contained no fish and trout streams contained brook trout throughout the experiment. Addition streams were fishless until I added brook trout following the 2002 samples. N = 3.

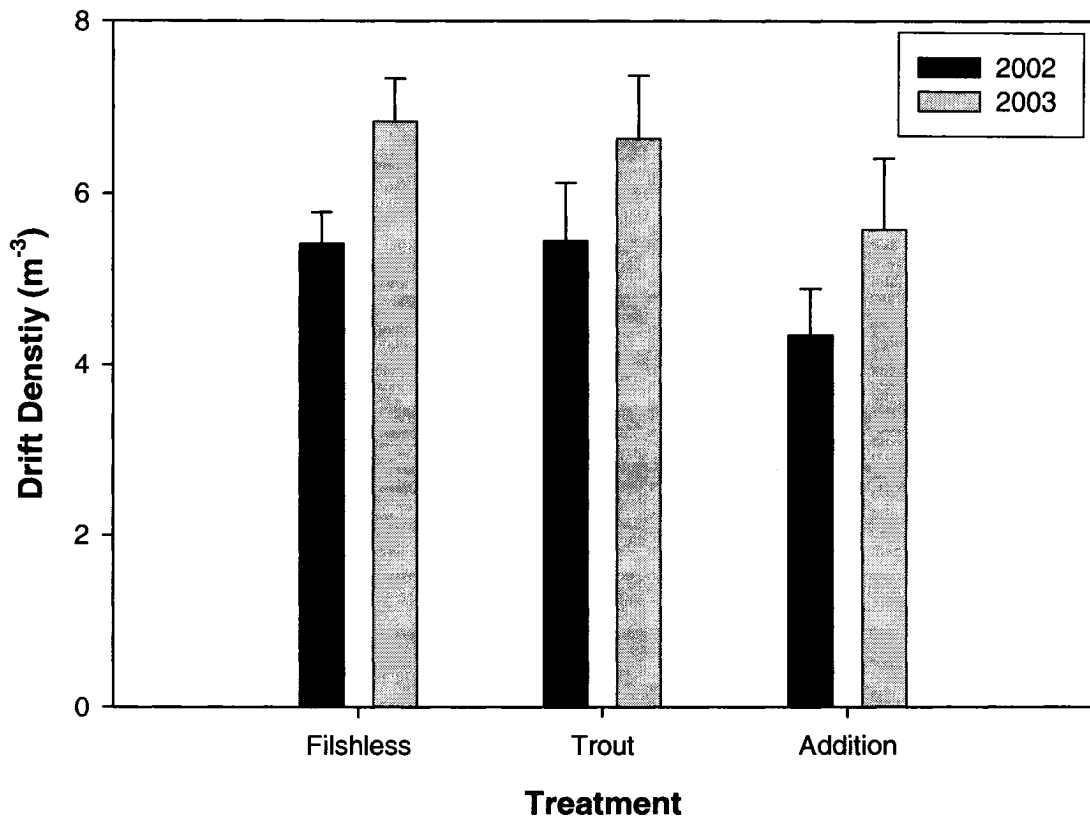


Figure 2-3: Mean (+ 1SE) invertebrate drift density among treatments in the July 2002 and 2003 samples in: fishless streams containing no fish and trout streams containing brook trout throughout the experiment, and addition streams that were fishless until I added brook trout following the 2002 samples. N = 3.

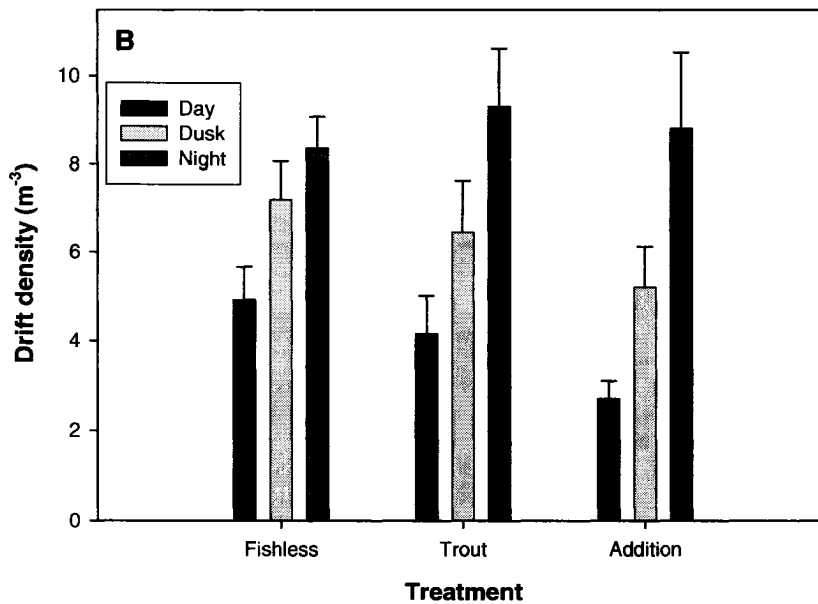
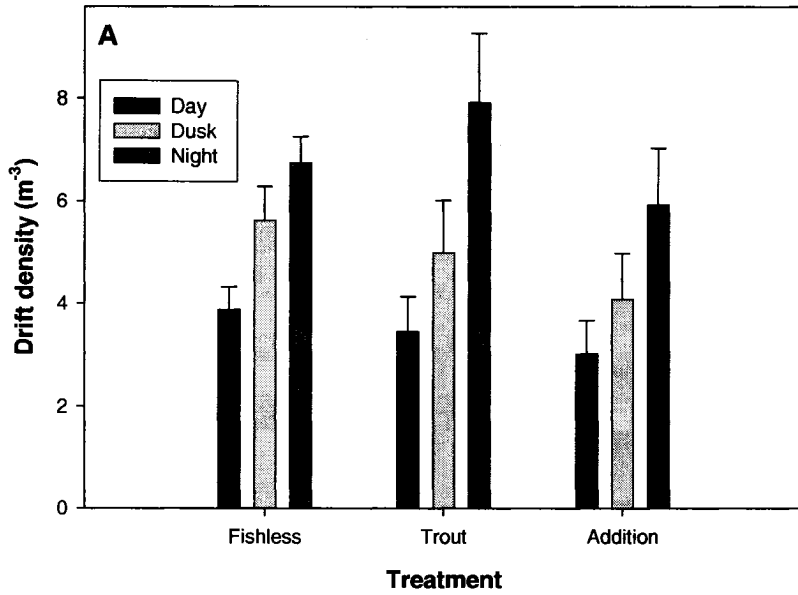


Figure 2-4: Drift density (+ 1SE) among treatments during day (~17-1900), dusk (~19-2100), and night (~21-2300) samples in A) July 2002 and B) July 2003. Fishless streams contained no fish and trout streams contained brook trout throughout the experiment. Addition streams were fishless until I added brook trout following the 2002 samples. N = 3.

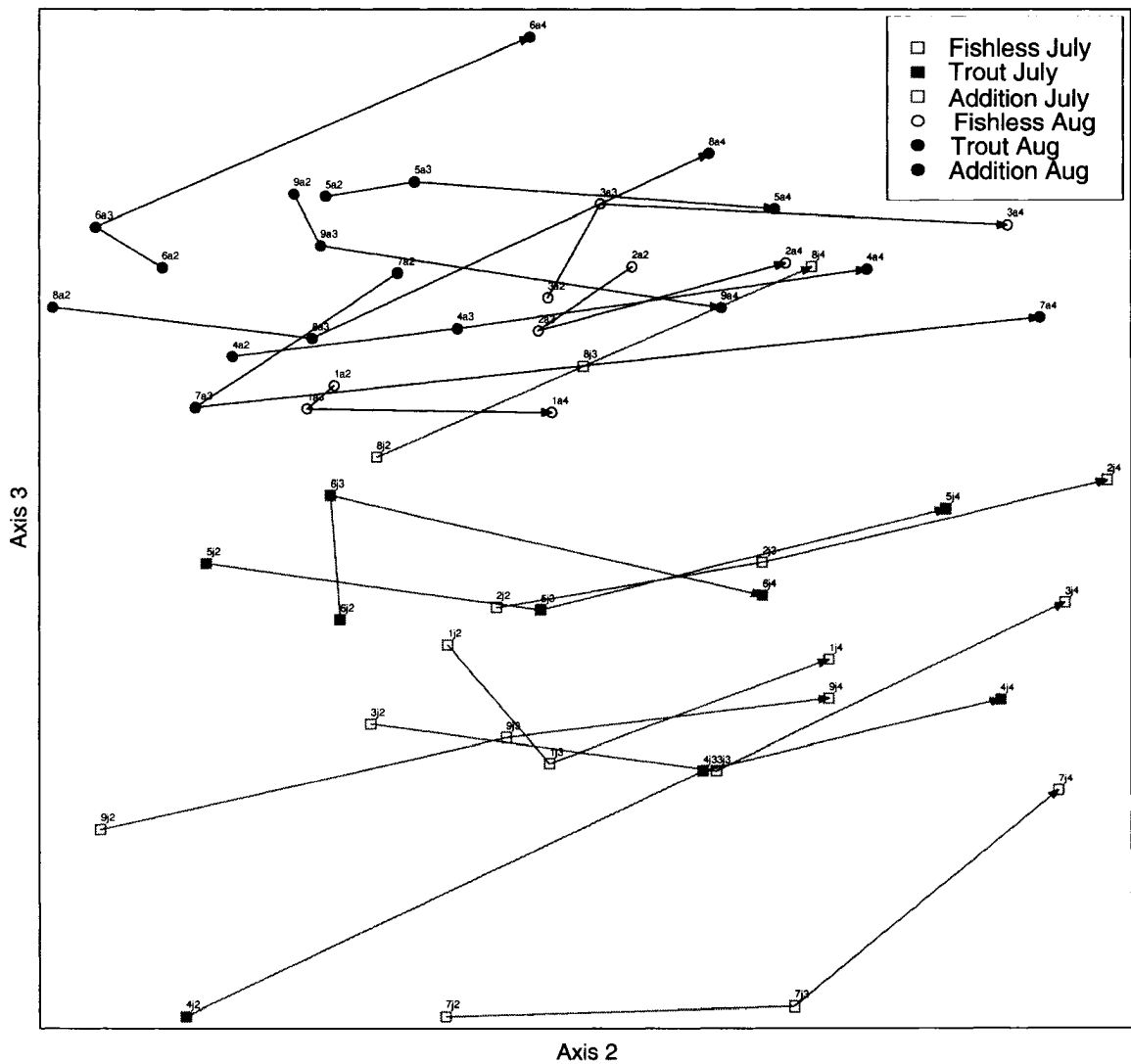


Figure 2-5. Scatterplot of samples across Axes 2 and 3 from the NMS ordination of invertebrate drift samples in July and August 2002. Lines show the movement of streams in ordination space from day, dusk, and night in July, before trout addition to addition streams, and August, after trout addition. The distances between points are proportional to dissimilarity in taxonomic composition.

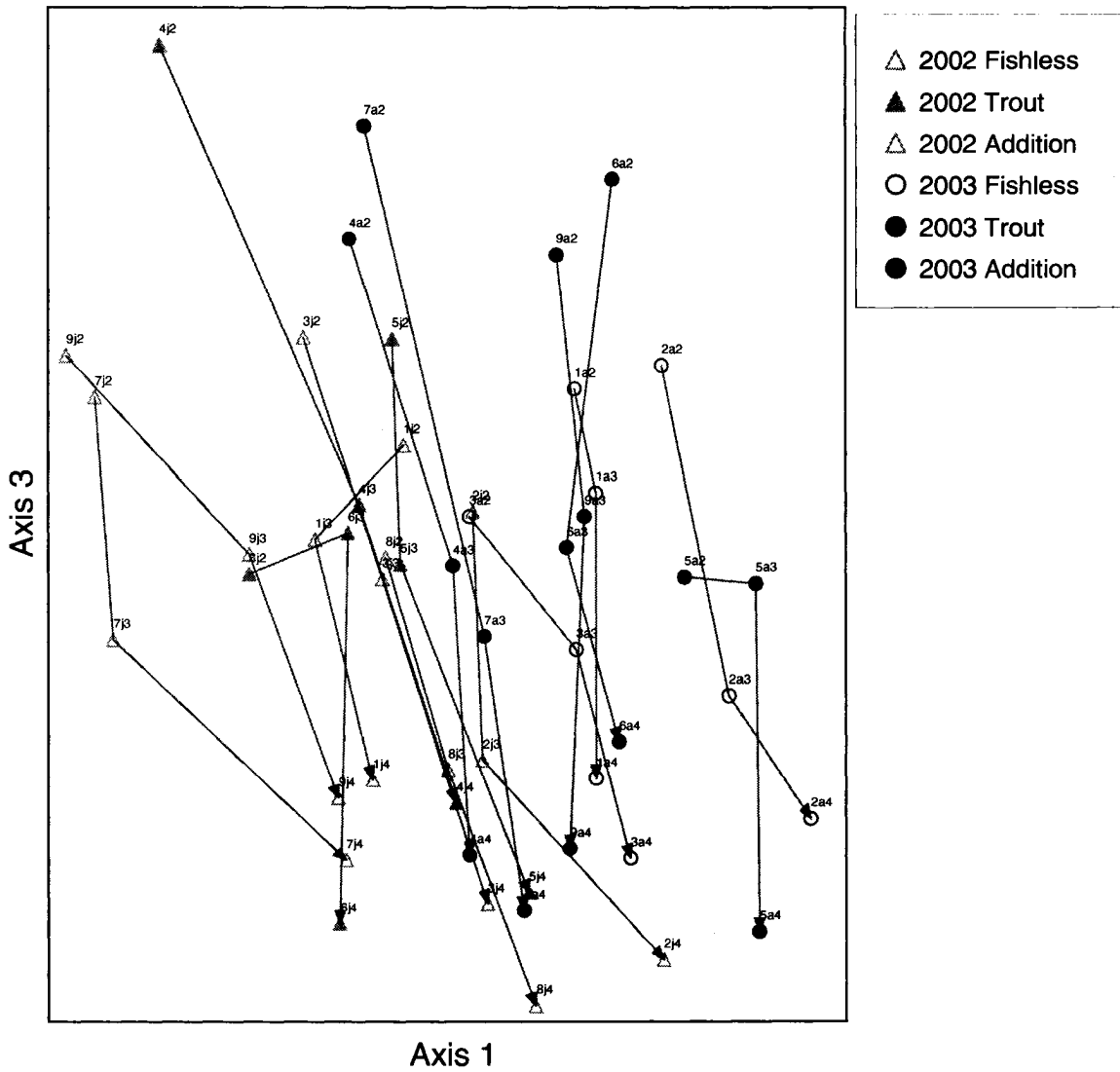


Figure 2-6. Scatterplot of samples across Axes 1 and 3 from the NMS ordination of drift samples in 2002 and 2003. Lines show the movement of streams in ordination space from day, dusk, and night in July 2002, before trout addition to addition streams, and July 2003, after trout addition. The distances between points are proportional to dissimilarity in taxonomic composition.

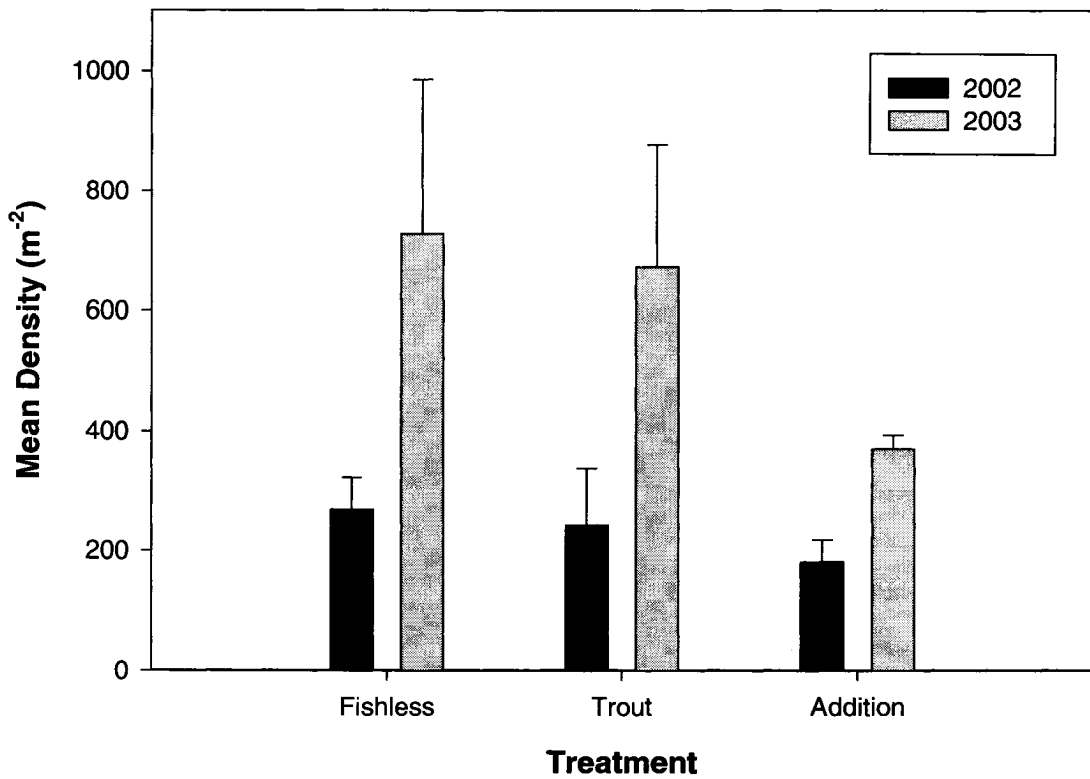


Figure 2-7. Mean (+ 1SE) invertebrate benthic density among treatments in July 2002 and 2003. Fishless streams contained no fish and trout streams contained brook trout throughout the experiment. Addition streams were fishless until brook trout addition following the 2002 samples. N = 3.

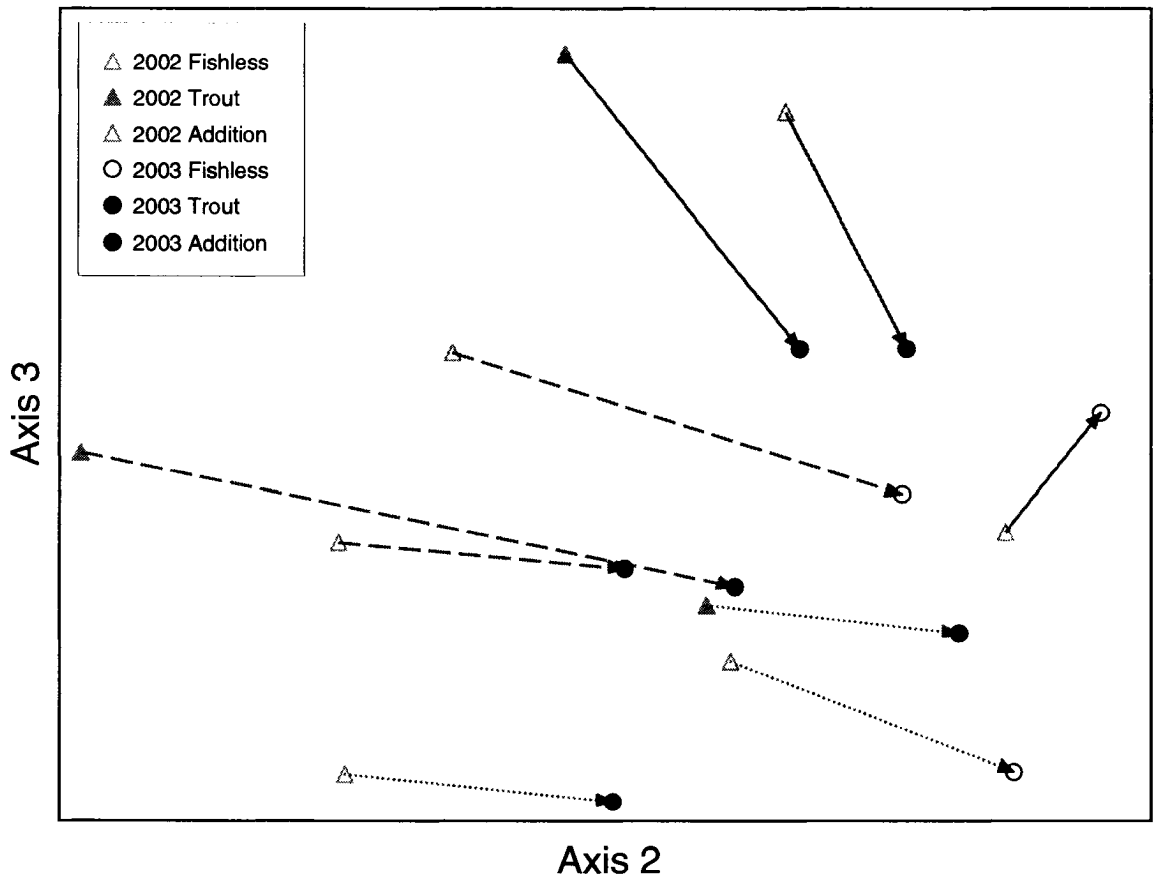


Figure 2-8: Scatterplot of benthic invertebrate samples in 2002 and 2003 across Axes 2 and 3 from the NMS ordination. Lines show the movement of streams in ordination space from 2002 to 2003 and are coded (solid, dashed, dotted) to reflect spatial blocks. The distances between points are proportional to dissimilarity in taxonomic composition.

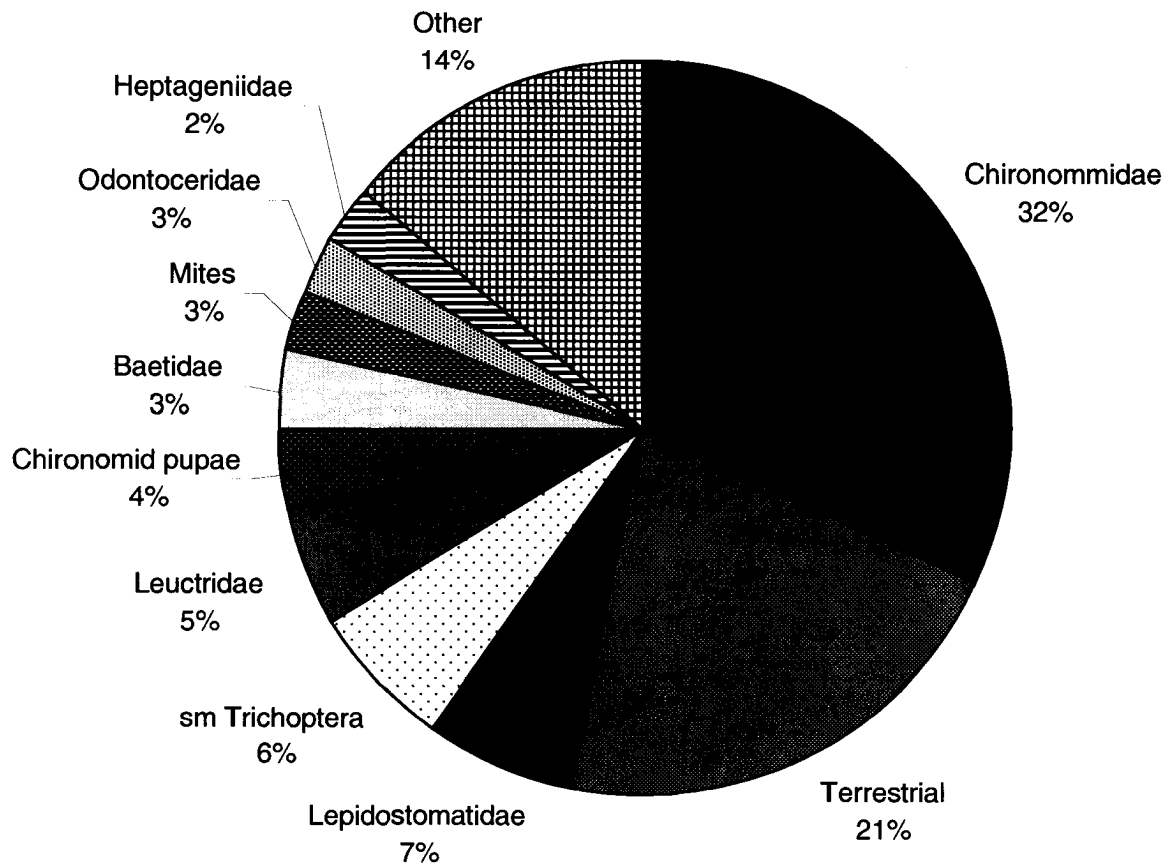


Figure 2-9: Stomach contents of brook trout in 3 streams in 2002 and 6 streams in 2003. Taxa that represented < 2% of stomach contents are combined as "Other."

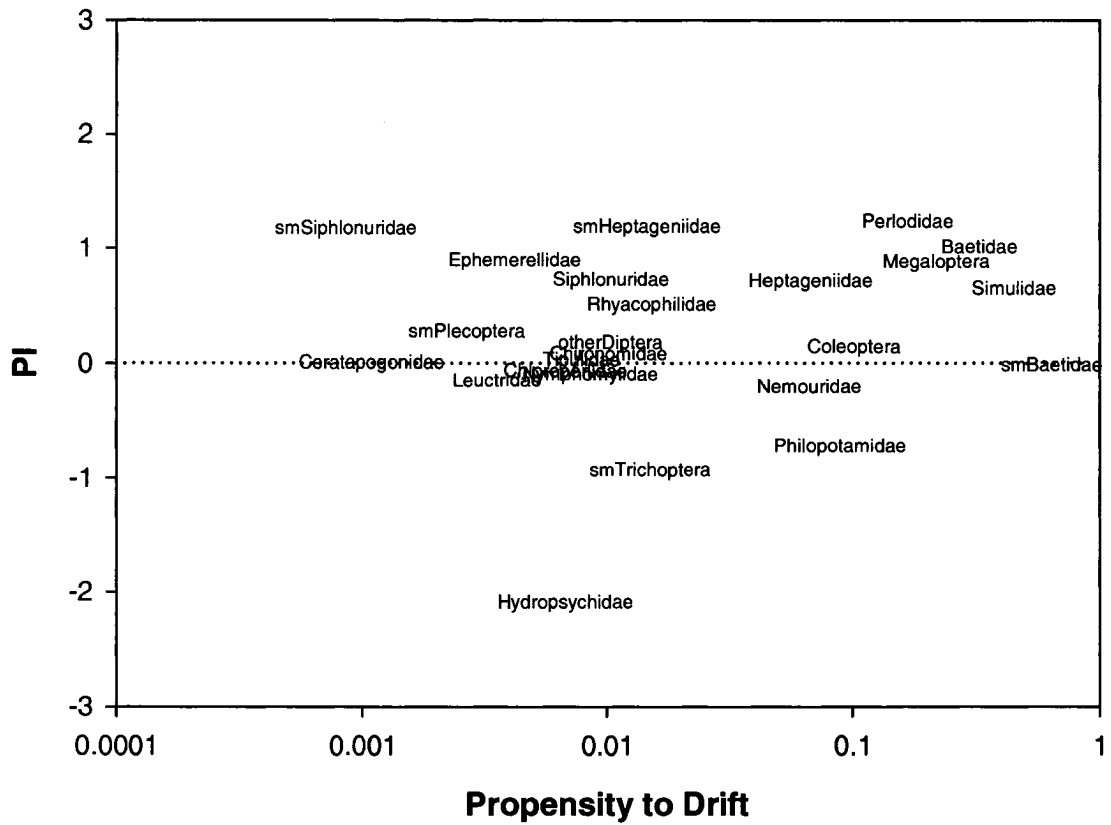


Figure 2-10: The relationship between the propensity to drift and the predator impact index (PI) of each taxon. Taxa with a negative PI are more abundant with trout than without.

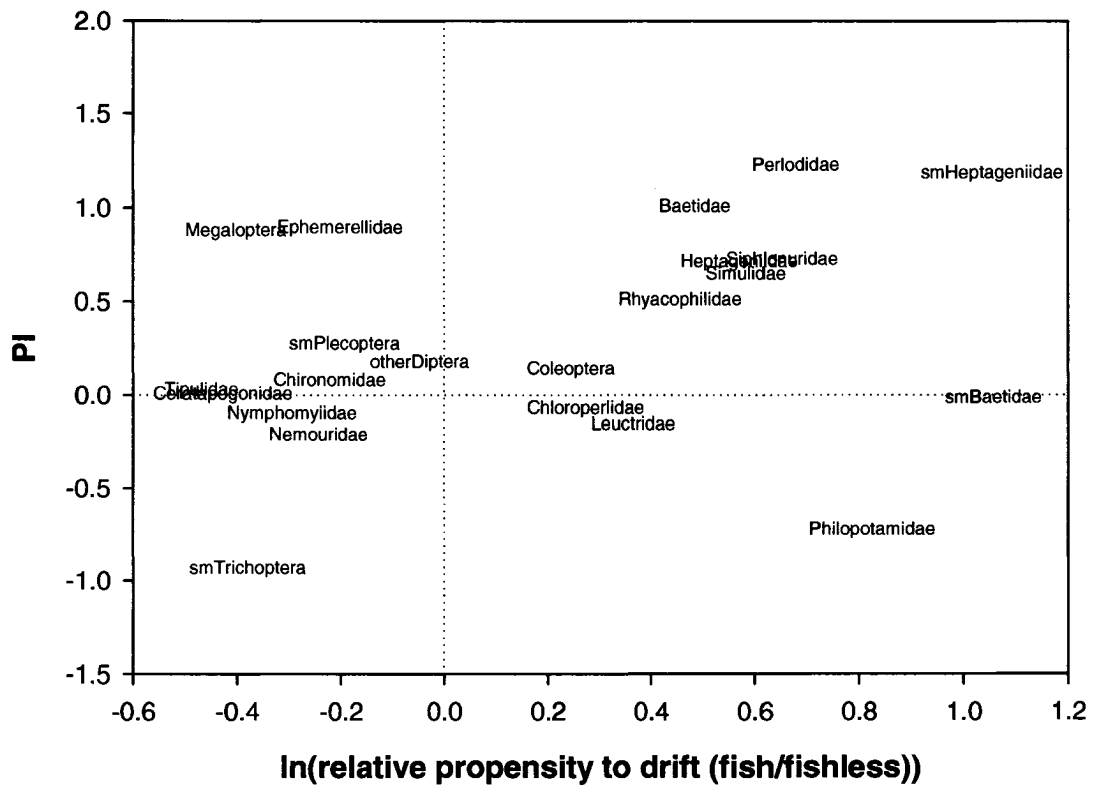


Figure 2-11: The relationship between the natural log of relative propensity to drift and the predator impact index (PI) for each taxon. Taxa with a negative PI are more abundant with trout than without. Taxa with a negative ln(relative propensity to drift) drifted less with fish than without; taxa with a positive ln(relative propensity to drift) drifted more with than without fish.

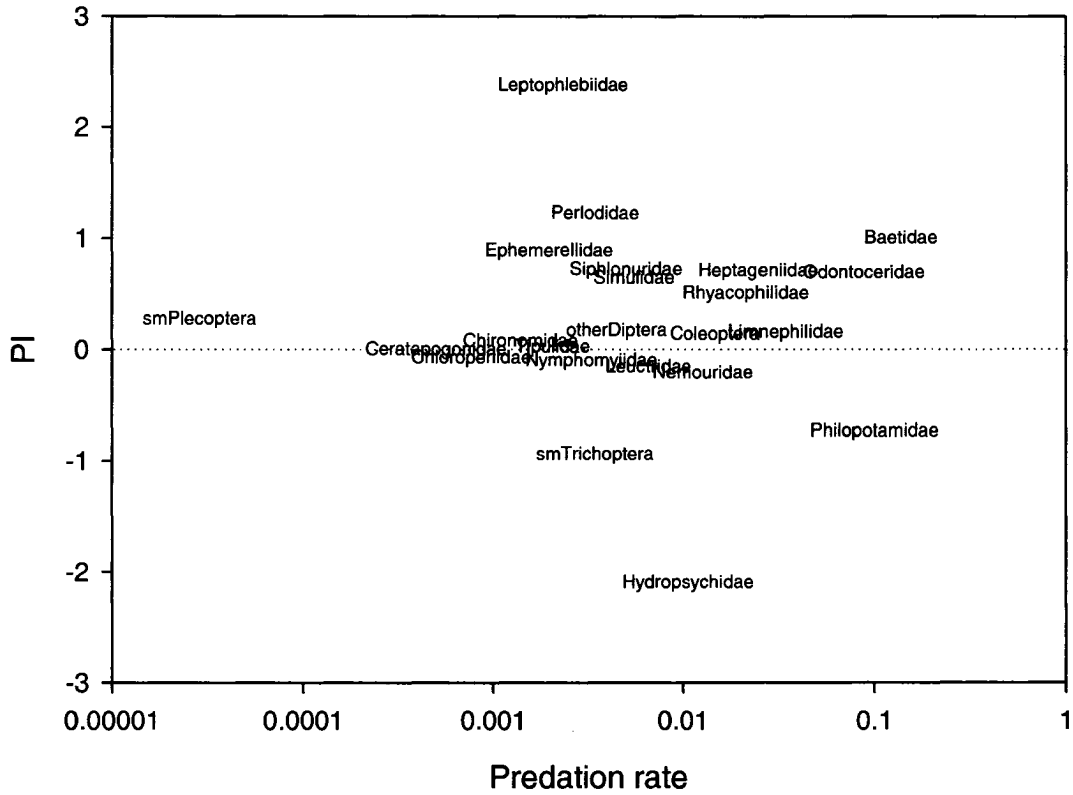


Figure 2-12: The relationship between brook trout predation rate (proportion in trout stomachs/ mean benthic density) and the predator impact index (PI) for each taxon. Taxa with a negative PI are more abundant with trout than without.

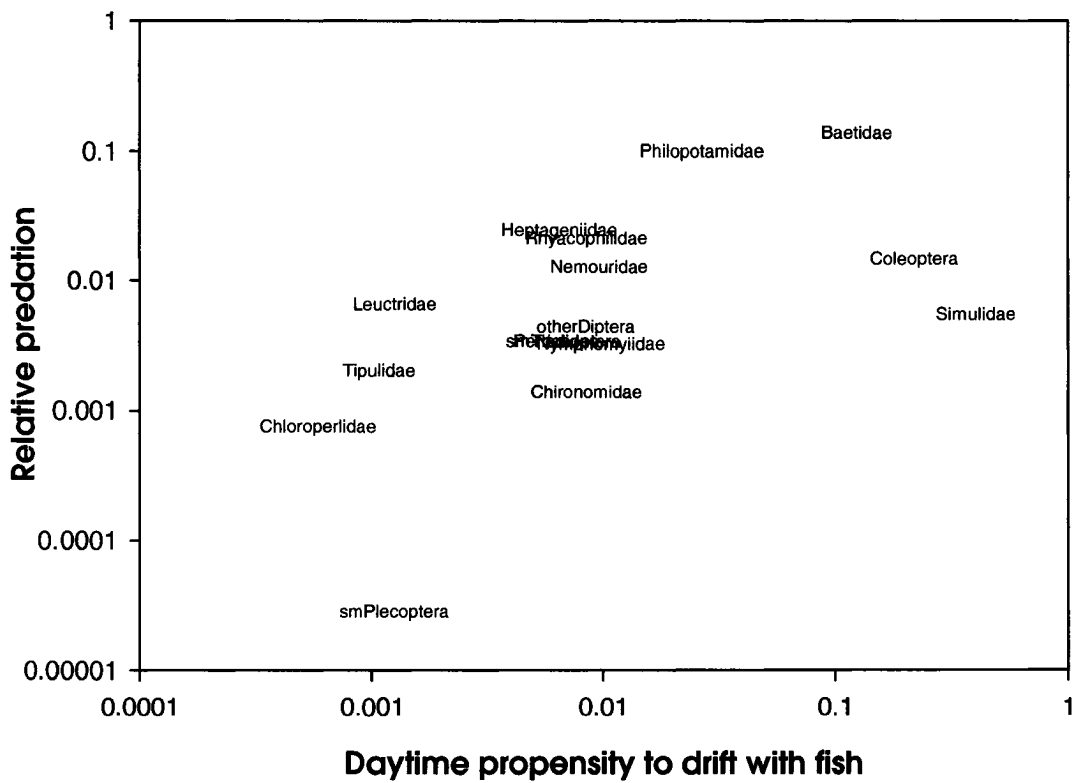


Figure 2-13: The relationship between propensity to drift and predation rate. Taxa with a negative PI are more abundant with trout than without.

CHAPTER 3

TROUT AFFECT THE DENSITY, ACTIVITY, AND FEEDING OF A LARVAL PLETHODONTID SALAMANDER

Introduction

A basic goal of ecology is to understand patterns in species' distributions and abundance and to elucidate underlying processes. Predation is one such process that can affect a species' abundance, and it has been a central goal of aquatic ecologists to understand the influences of predators on prey assemblages. Important to our understanding of predator-prey dynamics is the experimental simplification of natural systems in micro- and mesocosms using few species (Gause 1934, Lawler 1998). Advances using such simple systems are unmistakable, but it is clear that results from experimental microcosms do not necessarily translate to natural systems (Carpenter 1996, Peckarsky et al. 1997, McIntosh et al. 2002). For example, the negative impacts of fish on invertebrate prey abundance in small arenas are often not realized in large-scale studies, perhaps due to high rates of prey drift (Cooper et al. 1990, Englund 1997) or anti-predator behaviour (Sih and Wooster 1994).

Likewise, predicting the effects of multiple predators on prey using results from single predator-prey interactions can be misleading due to unexpected patterns of risk enhancement (facilitation) or reduction (interference) for the prey species (Vance-Chalcraft and Soluk 2005, Nilsson et al. 2006). Density-mediated interactions (DMI) may result if a predator reduces the density of another predator and indirectly increases prey survival. Trait-mediated interactions (TMI) may occur if a predator alters the behaviour of prey or another predator, resulting in an increase or decrease in prey mortality. Such interactions involving multiple predators are relevant to experimental ecologists because few organisms are faced with a single predator under natural conditions (Sih et al. 1998). Indeed, among the proposed explanations for the variation of predator impacts on their prey in streams and the difficulty of measuring predator impacts at large scales is the prevalence of multiple predators (Wooster et al. 1997, Sih et al. 1998).

salmonid fish are well-studied, cosmopolitan predators in freshwater systems. Although their apparent impacts on invertebrate assemblages in streams vary considerably among studies (Allan 1982, Bowlby and Roff 1986, Bechara et al. 1992), they can affect their invertebrate prey's activity (Huryn and Chivers 1999), drift density (McIntosh and Peckarsky 1999), drift periodicity (McIntosh and Peckarsky 1996, McIntosh et al. 2002), and benthic density (Bechara et al. 1992). Salmonids are typically

size-selective predators, and one of the more strong and general patterns of impacts in streams is their relatively pronounced impact on larger prey (Meissner and Muotka 2006). Furthermore, because many prey, including intermediate predators, often behaviourally respond to the presence of predators, there exists a likely potential of both trophic indirect effects (a DMI) and behavioural indirect effects (a TMI) on prey taxa.

Salamanders are another predator in freshwater systems and are abundant throughout headwater streams in the eastern (Beachy 1994, Petranka and Murray 2001, Barr and Babbitt 2002) and Pacific northwestern (Nussbaum 1977, Murphy and Hall 1981) United States. In the absence of fish, salamanders can be the dominant vertebrate predators, and their density can exceed 40 m⁻² (Nussbaum 1977, Huang and Sih 1991a, Beachy 1993, 1994, Barr and Babbitt 2002). Salamanders are rarely extirpated by fish (but see Petranka 1983, Gamradt and Kats 1996) but often coexist as intermediate or intraguild predators. In the presence of fish, salamanders can be less abundant (Resetarits 1997, Barr and Babbitt 2002), use different habitats (Resetarits 1991, 1995, Barr and Babbitt 2002) and alter refuge use (Kats et al. 1988, Sih et al. 1992). However, the interactions among salamanders, fish, and their shared invertebrate prey remain unclear. Some studies suggest salamanders are unimportant as predators in streams (Reice and Edwards 1986, Wooster 1998), but others document the effects of salamanders on invertebrate abundance (Davic

1983, Huang and Sih 1991a, Parker 1992), invertebrate behaviour (Huang and Sih 1991a), detrital processing (Davic 1983), and the growth and survival of smaller salamanders (Gustafson 1993, 1994, Beachy 1997, Rudolf 2006). Because of their abundance, salamanders may be important predators in stream systems, and their interactions with fish likely alter the roles of salamanders in stream systems.

In the White Mountains of New Hampshire, brook trout (*Salvelinus fontinalis* Mitchill) appear to be the dominant predator in most 1st and 2nd order streams, where they are typically the only fish (G.E. Barr and K.J. Babbitt, unpubl. data). However, fish are absent above many waterfalls and cascades that bar upstream movement in low-order streams. In these fishless reaches, two-lined salamander larvae (*Eurycea bislineata* Green) appear to be more abundant than with fish (Barr and Babbitt 2002), yet the effects of fish on their density and activity at a large spatial scale have not been tested. Of particular relevance to this and other freshwater systems are interactions among top and intermediate predators with their shared invertebrate prey. The direct impacts of predators on their prey's abundance can be relatively clear and straightforward. However, the more subtle effects of predators on the intermediate predator and prey's phenotype, such as behaviour or morphology, and resulting indirect effects can be of equal or greater importance (Werner and Peacor 2003, Preisser et al. 2005). In stream systems where ecologists have struggled to

find general patterns in the impacts of predators on their prey, recognizing the impacts of predators on the density and phenotype of intermediate predators and the resulting indirect effects on shared prey may be particularly relevant to understanding their impacts on macroinvertebrates at realistic spatial and temporal scales.

In this study of the interactions between two dominant vertebrate predators in New England stream systems, I examined patterns of two-lined salamander abundance in adjacent stream reaches above and below waterfalls, followed by a large-scale manipulation of brook trout presence. Our objective was to measure the impacts of trout on salamander density and activity at a large spatial-scale. I hypothesized that the density and activity of larval salamanders would be lower in the presence of trout and decrease following trout addition. I also conducted a small-scale laboratory experiment to study how brook trout and larval two-lined salamanders affect each other's prey consumption. I hypothesized that if salamanders are less active with trout, they would consume fewer prey in the presence than absence of trout.

Methods

I conducted this study in first and second order streams in the White Mountain National Forest, a 300,000 ha National Forest in northern New Hampshire and western Maine. Within the National Forest, elevation generally ranges from 300 to 1200 m with some peaks above 1500 m. Streams in the White Mountains are cold, clear, and low in nutrients and productivity (Hornbeck and Leak 1992). Allochthonous detritus dominates production in low order streams (Fisher and Likens 1973, Hall et al. 2001).

As a preliminary test of differences in salamander abundance in fish and fishless streams, I located 8 streams with waterfalls that function as barriers to upstream fish movement. To confirm the presence of fish below and absence of fish above the waterfalls, I electroshocked (Smith-Root model 12-B backpack, Vancouver, WA, USA) 100 m of each stream reach. I found no fish above but caught trout below the waterfall in all 8 streams. To estimate salamander abundance in the upper and lower (> 50 m from waterfall) reaches of each stream, I used time-constrained sampling in which 2 people searched multiple pools on hands and knees for 15 min, capturing every larval two-lined salamander encountered with a turkey baster (Barr and Babbitt 2001). A 30 x 15 x 9 cm plastic box with a Plexiglas bottom helped increase visibility through the uneven water surface.

Our large-scale field experiment included 9 streams: 3 with brook trout (fish stream), 3 without fish (fishless stream), and 3 without fish to which I added brook trout (addition stream). Of the fishless streams I located above waterfalls (8 sampled above and 11 later located), I used 6 for our experiment to form 3 spatial blocks, such that 2 fishless streams were relatively close to each other, had similar physiognomy, and were located near a similar stream with fish. Within each block, I randomly chose the fishless stream that would receive trout.

In fish and addition streams, I estimated fish density, using Zippin's (1958) equations, in a 100 m reach using a three-pass removal method with a backpack electroshocker. In each addition stream, I captured brook trout from below the waterfall and added them to an approximately 500 m reach above. This resulted in the relocation of 151 brook trout to a fishless reach in Crawford Brook (0.9 m^{-2} , 30-240 mm total length), 103 in Stony Brook (0.3 m^{-2} , 40-184 mm), and 149 in Steam Mill Brook (0.6 m^{-2} , 45-174 mm). Immediately following capture and enumeration, I packaged fish individually in plastic bags and transported them with backpacks. Trout were not restricted to their new stream reaches in any way, but sampling in 2003 showed that trout reproduced following relocation and maintained or increased their density. This field experiment would be unethical in many regions where fishless streams are rare and introduced trout pose a serious risk to natural systems. In this

mountainous region of New Hampshire, brook trout are native and waterfalls that block fish movement are common. Furthermore, upstream waterfalls restricted the expansion of trout in all 3 addition streams, thus our impact on the region's stream network was minimal.

For the large-scale field experiment, I measured larval salamander density and day and night activity in all 9 streams in July 2002 before adding trout to the 3 addition streams in late July and early August 2002. Immediately following trout addition to each of the addition streams, I measured day and night activity to determine whether salamander behavioural responses to fish were immediate. In 2003, I measured salamander density and day activity in all 9 streams. To measure salamander density and activity, I sampled one 0.5 m² quadrat in each of 8 pools randomly chosen from 15 in each stream and randomly placed quadrats where the water was no deeper than 1 m and the substrate was dominated by pebbles and cobbles. I estimated surface activity as the number of larvae visible within the quadrat before disturbing substrate particles and measured density as the surface activity plus the number captured while removing substrate particles larger than a pebble (>64 mm). I used an incandescent light for nighttime samples and did not measure nighttime activity within 4 days of a full moon.

I conducted our lab experiment in 76 l glass tanks in a lab at the Bartlett Experimental Forest, Bartlett, New Hampshire. Plexiglas baffles and

an air wand were used to create circulating flow, and brown cardboard and 1.9 cm foam insulated and visually isolated the tanks. I used a substitutive experimental design, whereby the prey consumption of each predator species was measured in single-species low-density, single-species high-density, and mixed-species, each at low-density, treatments. Thus for each 20 hr trial (from 1830 to 1430 the following day), tanks contained: 2 two-lined salamander larvae, 4 two-lined salamander larvae, 1 brook trout, 2 brook trout, or 2 two-lined salamander larvae with 1 brook trout. This design is appropriate because it accounts for nonlinearities in predator-prey interactions (Sih et al. 1998). Each of 5 treatments was run on 5 consecutive days for a total of 5 replicates of each treatment.

Each tank contained a natural mix of sand, gravel, pebbles, and cobbles with a natural density and composition of benthic invertebrates collected together with a Surber sampler. The mean density of invertebrates collected with a vacuum sampler in riffles across eight streams in July 2002 was $700 \pm 55 \text{ m}^{-2}$ ($\bar{x} \pm 1\text{SE}$), thus I assumed that the potential influence of prey depletion was minimal in this experiment. I used separate aquaria for treatments with and without fish and randomized the spatial arrangement of tanks for each trial, but the water and substrate came from a fish-occupied stream. I collected salamander larvae with a turkey baster from small fishless tributaries and trout with a

backpack electroshocker. Before each trial, trout and salamanders were held for approximately 24 hrs in stream enclosures without access to food. I added the substrate (with invertebrates), larval salamanders, and trout at 30 min intervals to allow acclimation. Trout and larval salamanders were preserved in 70% ethyl alcohol for later dissection and enumeration of stomach contents.

I used relatively large salamander larvae (44.4 ± 0.9 mm total length; mean \pm SE) and small brook trout (58.0 ± 1.1 mm total length) in the experiment to avoid salamander mortality. Preliminary observations suggested that large salamander larvae are beyond the gape-limits of small brook trout (thus no salamander mortality) but respond equally to trout of all sizes by increasing refuge use. As a test of our observations, I measured the survival and behaviour of 3 salamander sizes with 3 trout sizes. The 48 hr experiment was a randomized complete block design with 4 replicates in 35 x 22 x 14 cm plastic bins in a lab at the Bartlett Experimental Forest. Each bin contained: 1 large (~ 15 cm) and a cluster of 5 small cobbles (~ 8 cm), 10 salamander larvae, 1 trout, and an air stone. I used individuals from the center of naturally occurring size classes of two-lined salamanders (small, 22 to 28 mm total length; medium, 34 to 42 mm; and large 46 to 54 mm) and brook trout (small, 4.1 to 4.7 cm total length; medium 7.8 to 8.8 cm; and large, 10.9 to 11.8 cm).

Confirming our preliminary observations, larval salamanders were nearly always found under cover objects during the day, across all treatments; larvae used the entire tank and move in the open when trout were absent (pers. obs.). Despite the low to no risk of mortality in the presence of small brook trout (Figure 3-1), even large salamander larvae restricted their activity to under cobbles. "Survival" of large salamanders was not 100% because one individual crawled out of its tank.

To test patterns in salamander abundance above and below the 8 sampled waterfalls, I used a paired t-test. For the field experiment, I analyzed the change (2003 minus 2002) in larval salamander density and activity (mean of 8 plots per stream) among treatments with Analysis of Variance (ANOVA) using a spatial block according to the arrangement of streams in the landscape. I used a Multivariate Analysis of Variance (MANOVA) for a repeated measures test (Wilkinson et al. 1996) of the change in salamander activity among daytime and nighttime observations made before and after trout addition and a Tukey's test for comparisons of the cell means. I used per capita activity (arcsine square root transformed) and the change in density to account for differences in salamander density among streams. I tested for differences in the number of prey consumed per predator among the density treatment and predators using log transformed data in a blocked (by trial) two-factor

ANOVA. Statistical analyses were performed with SYSTAT 11 (SPSS, Evanston, IL, USA).

Results

Larval two-lined salamanders were less abundant below waterfalls (with trout) than above waterfalls (without trout; $t_7 = -8.42$, $p < 0.001$; Figure 3-2). In all 8 streams, larvae were less than half as abundant below the waterfall than above. Similarly, salamander abundance decreased following the addition of trout during our field experiment. From 2002 to 2003, larval salamander density decreased in 8 of the 9 streams; 2002 was a dry year, thus salamanders may have been confined to a smaller stream bed than in 2003, which received high July rainfall. The decrease in salamander density from 2002 to 2003 was greater in addition than in fish streams ($F_{2,4} = 21.9$, $p = 0.007$; Tukey $p = 0.006$). The difference between addition streams and fishless streams was marginally significant (Tukey $p = 0.06$; Figure 3-3).

Daytime surface activity of larval two-lined salamanders decreased in all treatments following trout addition. The decrease in activity was greater in streams to which trout were added than streams with trout ($F_{2,4} = 8.55$, $p = 0.04$). The difference between addition and fishless streams was marginally significant (Tukey, $p = 0.06$; Figure 3-4).

In the 3 addition streams, larval salamander surface activity decreased after trout addition ($F_{1,4} = 29.3$, $p = 0.006$). Time of day was not a significant factor alone ($F_{1,4} = 1.6$, $p = 0.27$); however, the significant interaction between the time of day and presence of trout ($F_{1,4} = 9.5$, $p = 0.037$) and pair wise comparisons indicate that salamander larvae shifted their activity from aperiodic to more nocturnal following trout addition (Figure 3-5).

During the laboratory experiment, larval salamanders consumed more prey (3.65 ± 0.48 ; $\bar{x} \pm SE$) than did fish (1.9 ± 0.47 ; Table 3-1). All fish and salamanders survived, and 5 fish and 3 salamanders had no prey in their foreguts, which I included in the analyses. The predator by density treatment interaction was significant (Table 3-1), indicating that the effect of the density treatment was not consistent across the 2 predator species. Whereas consumption by larval salamanders did not differ between the low and high density treatments, they ate fewer prey in the presence of fish. In contrast, trout ate more in the presence of a conspecific than alone and still more prey in the presence of larval salamanders (Figure 3-6).

Discussion

Measuring the effects of predators on prey abundance in streams has been a difficult endeavor, particularly in relatively large-scale studies (Allan 1982, Forrester 1994). However, predators, such as trout, tend to show greater or more easily measured impacts on larger prey (Meissner and Muotka 2006). As expected in our study, trout reduced the density of larval salamanders. I found fewer salamanders: in streams with trout than without fish, below waterfalls with trout than above without fish, and 1 yr following the addition of trout than before. This and previous studies (Petranka 1983, Sih et al. 1992, Barr and Babbitt 2002, Lowe et al. 2004) suggest there is a common, direct effect of fish on stream salamander abundance. Lower salamander abundance with fish may have important implications for prey assemblages in many headwater stream systems. Fish can be the dominant vertebrate predator, but in smaller streams where fish are excluded by waterfalls or other barriers, salamanders are more abundant (3 times more abundant above waterfalls in our study). As abundant predators in the absence of fish, salamanders are likely have a relevant impact on invertebrate assemblages and can confound comparisons of invertebrate density among streams with and without fish.

Furthermore, behaviourally-mediated interactions appear to affect prey consumption by trout and salamanders. Previous research suggested that larval two-lined salamanders use refuges during the day to avoid

predators (Johnson and Goldberg 1975, Petranka 1984), yet I know little of their behavioural responses to trout. Our data show that in the absence of fish, when the risk of predation is apparently low, larval two-lined salamander activity on the substrate surface is aperiodic. In the presence of trout, salamanders reduce their daytime activity and are more active at night when foraging is relatively safe. Such reduced activity is likely a key mechanism for persistence with fish but is often linked to a tradeoff with energy intake (Lima 1998, Werner and Peacor 2003, Preisser et al. 2005). Our lab experiment confirms that the decrease in two-lined salamander surface activity in the presence of trout results in decreased prey capture. Therefore, in the presence of trout, salamanders are less abundant and appear to consume fewer prey.

In contrast to the interference of trout with salamanders, salamanders appear to facilitate trout feeding. Trout ate over six-times more prey in the presence than absence of salamanders. Similar patterns of facilitation can occur between predatory stonefly nymphs and both trout and sculpins (Soluk and Collins 1988c, Soluk and Richardson 1997). In experimental stream channels, trout even lost weight in the absence of stoneflies but gained weight in their presence (Soluk and Richardson 1997). As in our experiment, stonefly facilitation of fish predation on smaller invertebrates was trait-mediated because the intermediate predators were too large for trout to consume. Such research suggests that

interactions between salamanders and trout not only have implications for salamander populations and macroinvertebrates but that the presence of salamanders is relevant to trout populations and native fisheries.

The facilitation of trout foraging combined with the effects of trout on larval salamander abundance, activity, and feeding may affect stream invertebrate assemblages. In the absence of trout, larval salamanders can reach high densities and likely consume a non-trivial portion of benthic invertebrates (Davic 1983, Parker 1992), but in the presence of trout, larval salamanders are less abundant and eat fewer prey. The density-mediated impact of trout on salamanders likely has a positive, indirect trophic effect on stream invertebrates. The behavioural interactions among trout, salamanders, and their shared invertebrate prey enhance trout predation but reduce salamander predation. Combined, the above interactions represent a complex suite of processes that are likely important in stream systems and may influence our ability to measure the impacts of predators on macroinvertebrates. Further research should include measures of trout and salamander feeding *in situ* and the effects on trout growth and salamander growth and metamorphosis.

Salamanders are abundant components of stream systems throughout the eastern and Pacific Northwestern United States. The

negative effect of fish on salamander abundance and the behavioural responses to predators seem common, thus the reduced abundance of salamanders with fish as observed in this study may be quite general. Likewise, most larval stream salamanders appear able to detect chemical cues from predators (Petranka et al. 1987, Kats et al. 1988, Rundio and Olson 2003), thus I suspect the behavioural avoidance of fish by salamanders is common in taxa with historic exposure to fish (Kats et al. 1988). Such responses are likely critical to their persistence with fish and may affect feeding as demonstrated in our laboratory experiment with two-lined salamanders. However, the generality of such patterns among salamander species deserve careful attention. Despite reports of the impacts of fish on stream salamander abundance, patterns can vary among species (Resetarits 1997) and by life-stage (Lowe et al. 2004). Of particular relevance may be the differences between larval and adult salamanders as predators and prey. As prey, adults may be less vulnerable to fish due to their larger size and available refuge in adjacent terrestrial habitats. Indeed, larval spring salamanders (*Gyrinophilus porphyriticus* Green) appear to be less abundant with trout but adults are more abundant or show no clear relationship to trout presence (Resetarits 1997, Lowe et al. 2004). When viewed as predators, focusing on adults will often underestimate the role of salamanders because adults of many species are ineffective predators under water. The hyobranchial

apparatus that expands the buccal cavity for suction feeding in larvae is altered at metamorphosis to protract the tongue pad in adults (Deban and Marks 2002), which benefits terrestrial prey capture but prohibits adults from suction feeding. The poor feeding success of adult plethodontid salamanders in water is supported by Pasachnik and Ruthig (2004) who found that adult two-lined (*E. b. cirrigera*) and dusky (*Desmognathus fuscus* Rafinesque) salamanders tended to only maintain weight while housed in underwater enclosures yet gained weight in stream bank and forest habitats. Similarly, previous research using adult two-lined salamanders as predators in streams has tended to marginalize their impacts by reporting no impact of salamanders on invertebrate prey (Reice and Edwards 1986, Wooster 1998). Studies addressing the impacts of salamanders on stream invertebrates should use larval salamanders in most cases.

Ecologists have struggled to describe general patterns in the impacts of predators on stream prey, particularly at large, realistic spatial and temporal scales. Among the confounding variables in many systems is the presence of multiple predators whose interactions can be complex and unpredictable. Due to the abundance of salamanders in many systems and in light of our results showing the effects of fish on salamander abundance, activity, and feeding, I suggest the roles of salamanders as predators in streams deserve closer attention.

Table 1: ANOVA table for the comparison of prey items per stomach of brook trout and larval two-lined salamanders among single species treatments at low and high density and mixed species treatment with each at low density.

Source	SS	df	MS	F	p
Block (Trial)	30.80	4	7.70	2.89	0.049
Density Treatment	4.21	2	2.11	0.79	0.47
Predator	17.25	1	17.25	6.48	0.019
Treat × Pred	26.38	2	13.19	4.95	0.018
Error	53.27	20	2.66		

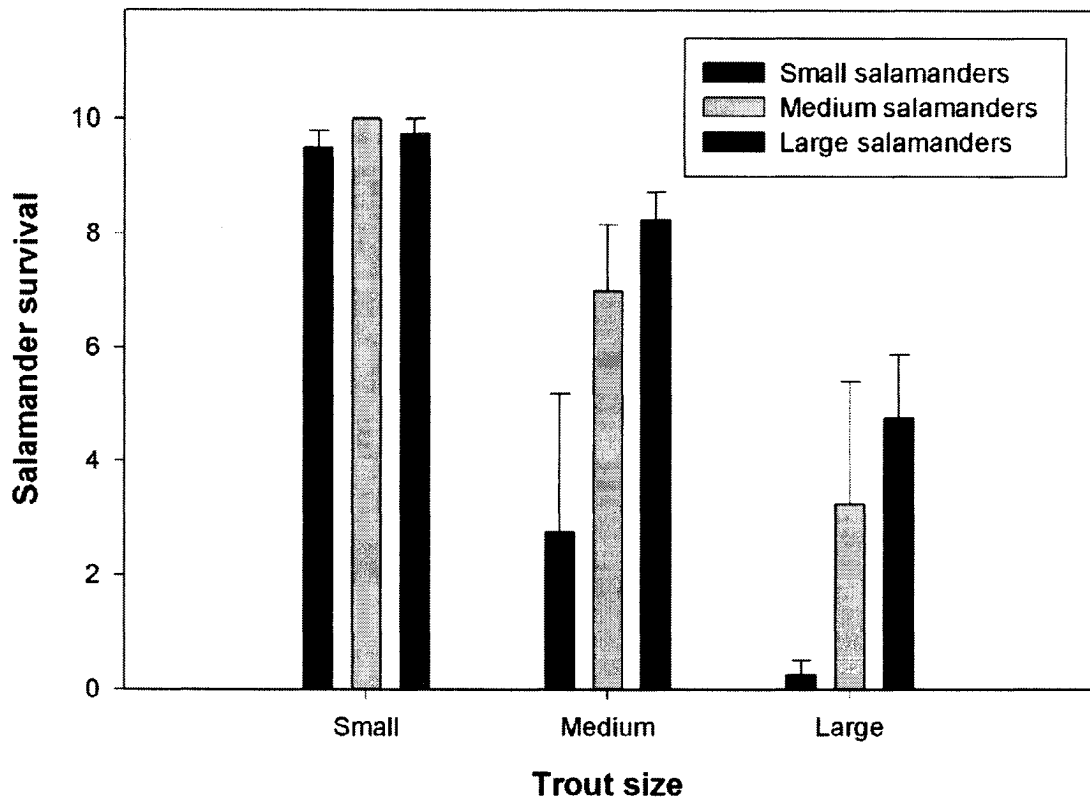


Figure 3-1: Survival (mean + 1 SE) of 3 sizes of larval two-lined salamanders with 3 sizes of brook trout. Survival of larval salamanders with brook trout was affected by salamander size ($F_{2,24} = 38.08$, $p = 0.007$) and trout size ($F_{2,24} = 147.25$, $p < 0.001$). The interaction between salamander size and trout size was not significant. All pair wise comparisons within factors were significant (Tukey; $\alpha = 0.05$) except medium vs. large salamander survival. $N = 4$

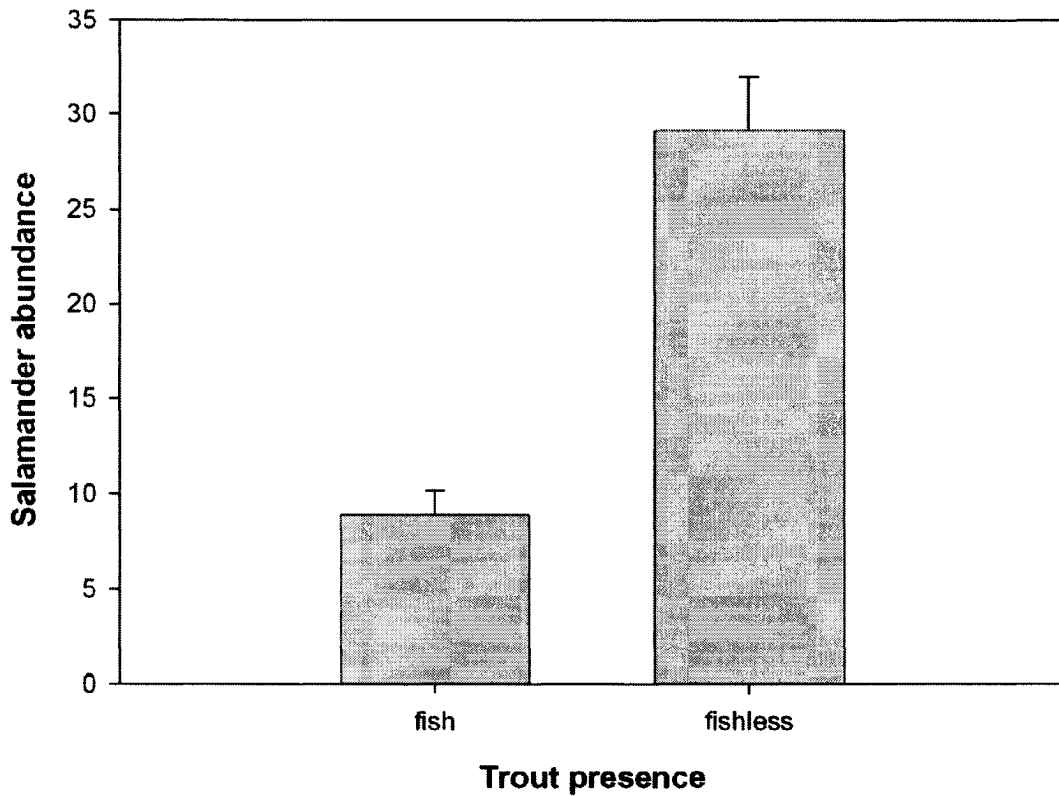


Figure 3-2: The abundance (per 0.5 person-hrs) of larval two-lined salamanders below waterfalls with brook trout and above waterfalls without fish. N = 8 streams.

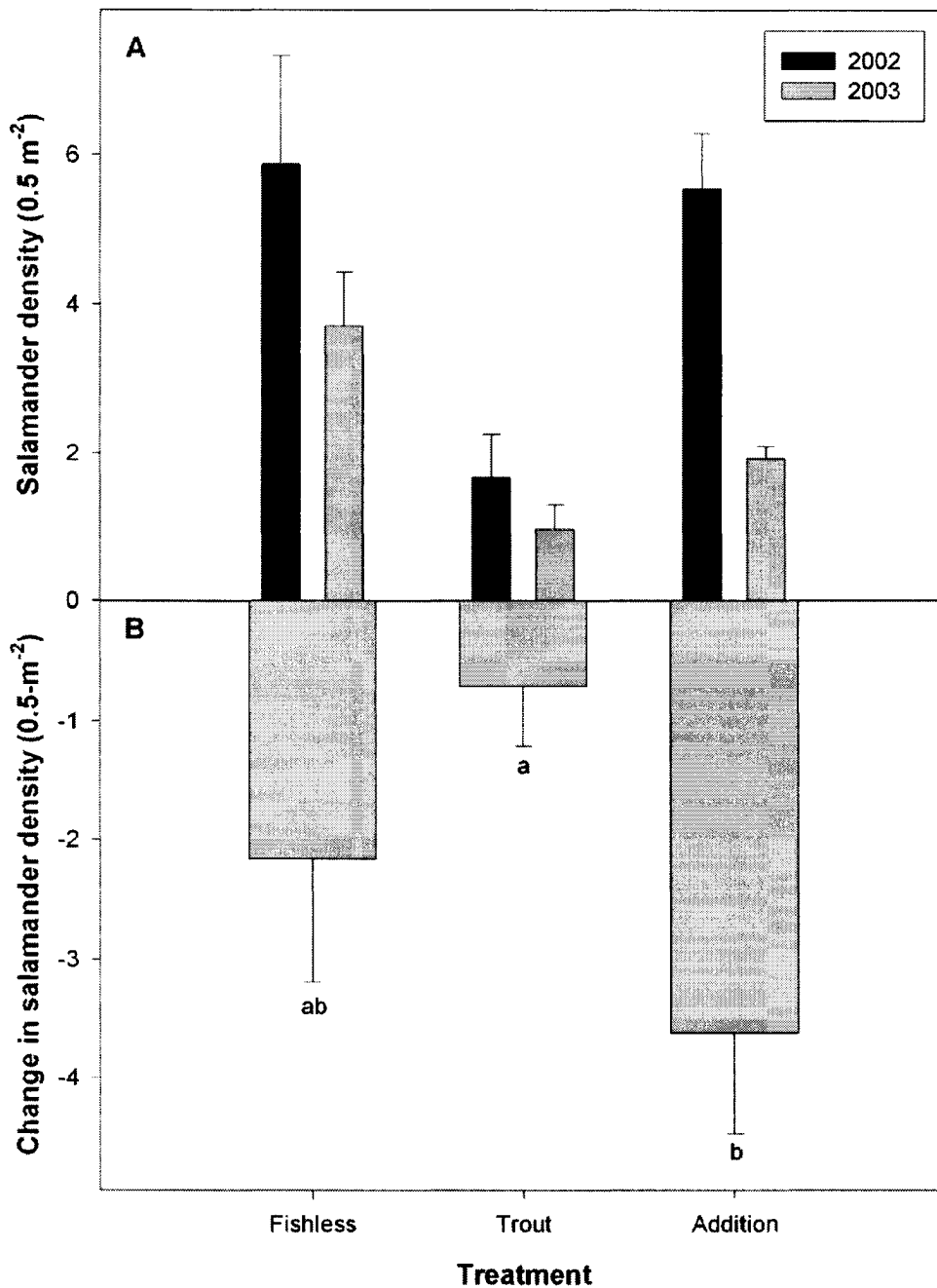


Figure 3-3: The density (mean + 1 SE) and change in density (mean - 1 SE) of larval two-lined salamanders in: fishless streams containing no fish and trout streams containing brook trout throughout the experiment, and addition streams that were fishless until I added brook trout following the 2002 samples. A) Larval salamander density in 2002 and 2003 samples. B) Change in larval salamander density from 2002 to 2003. Bars labeled with the same letter do not differ significantly at $\alpha = 0.05$. $N = 3$

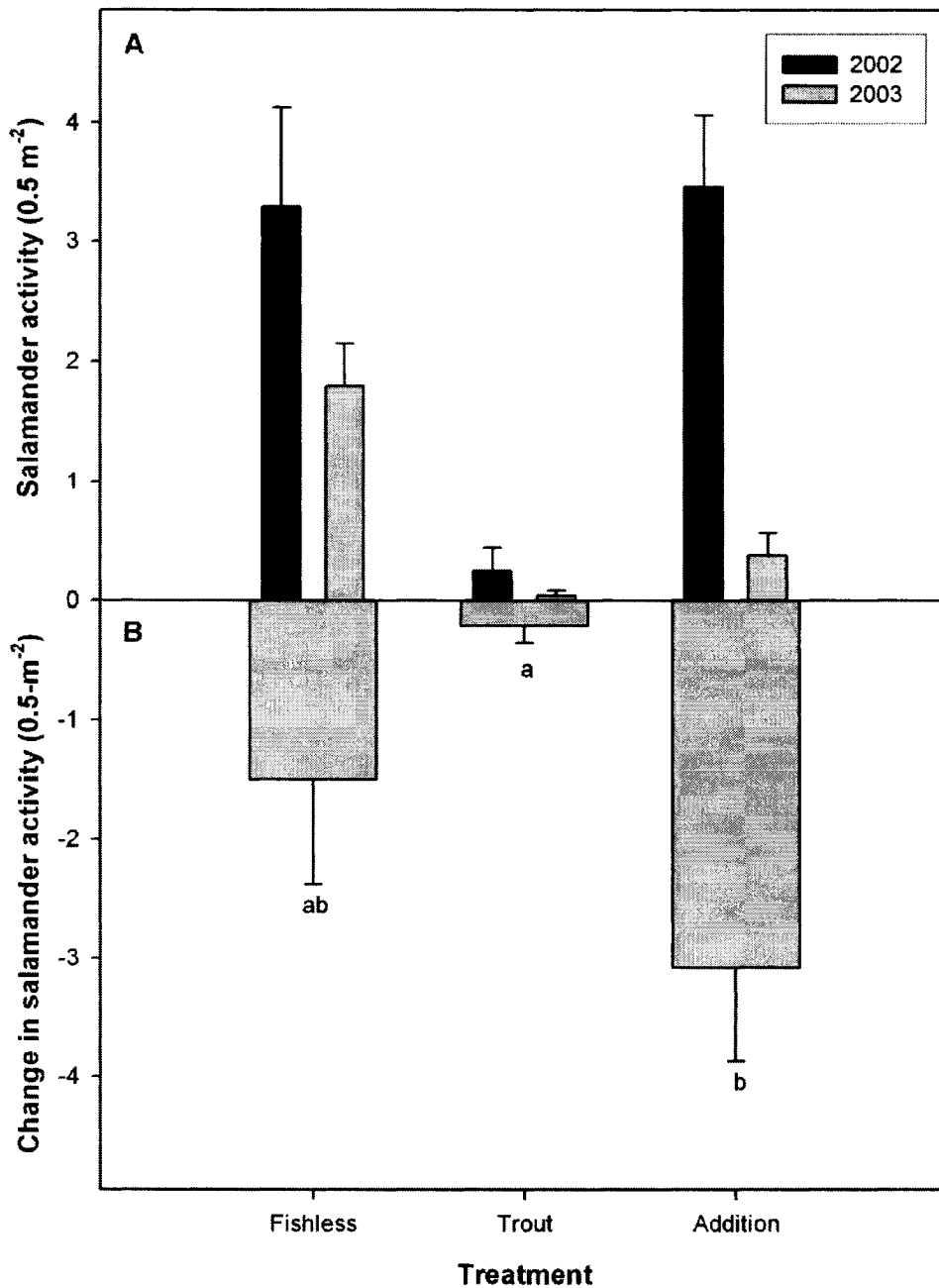


Figure 3-4: The activity (mean + 1 SE) and change in daytime surface activity (mean - 1 SE) of larval two-lined salamanders in: fishless streams containing no fish and trout streams containing brook trout throughout the experiment, and addition streams that were fishless until I added brook trout following the 2002 samples. A) Larval salamander activity in 2002 and 2003 samples. B) Change in larval salamander activity from 2002 to 2003. Bars labeled with the same letter do not differ significantly at $\alpha = 0.05$. N = 3

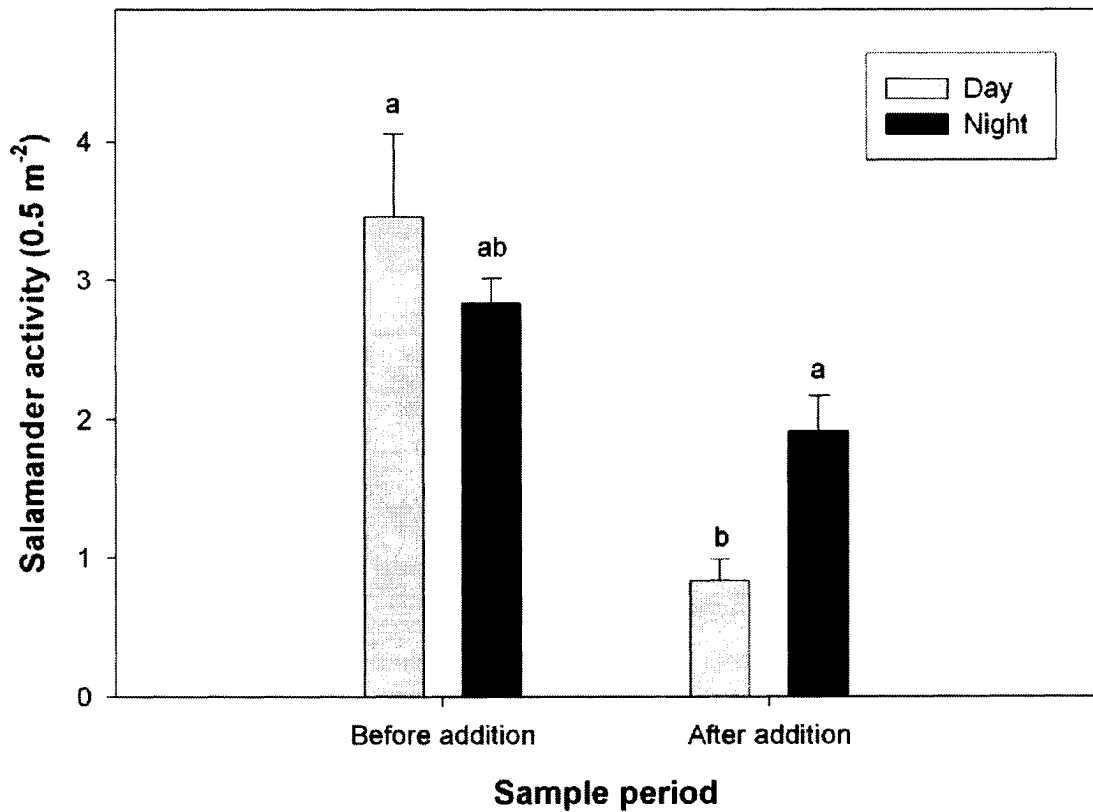


Figure 3-5: Day and night surface activity (mean + 1 SE) of larval two-lined salamanders before and after addition of brook trout. Bars labeled with the same letter do not differ significantly at $\alpha = 0.05$. N = 3

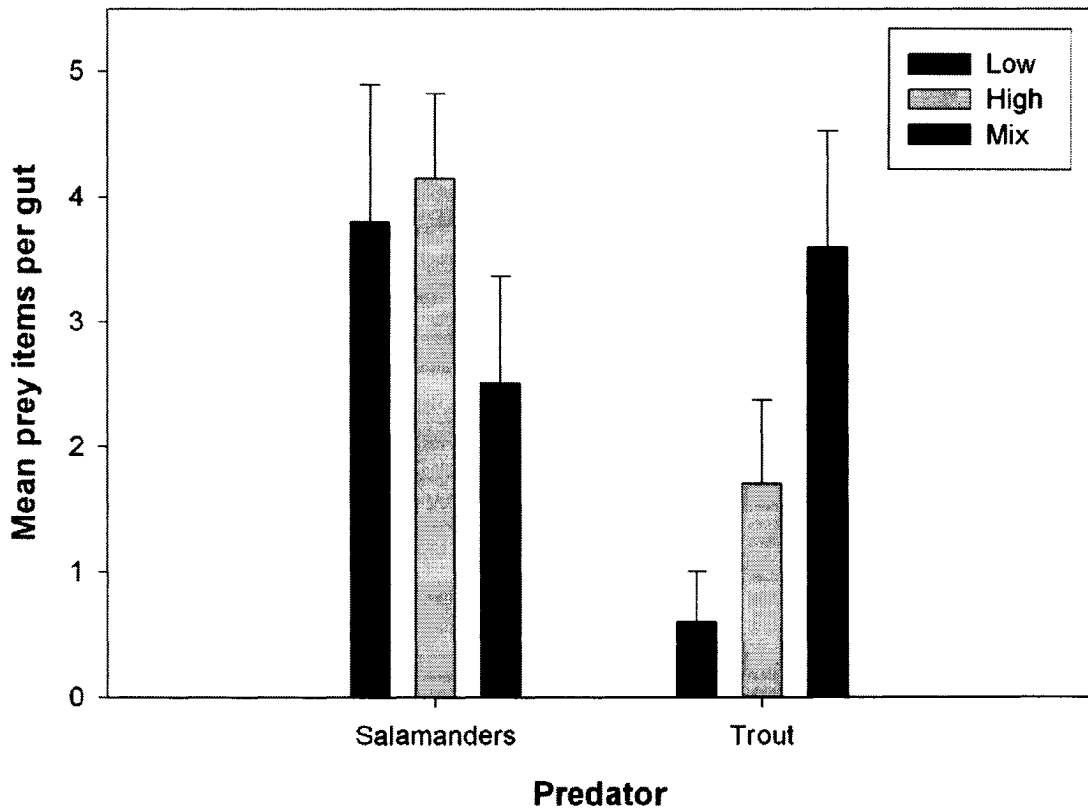


Figure 3-6: Mean (+ 1SE) invertebrates per gut for the comparison of prey items per stomach of brook trout and larval two-lined salamanders among single species treatments at low and high density and mixed (mix) species treatment with each at low density. N = 5.

CHAPTER 4

CONCLUSION

Stream systems are notoriously variable, spatially and temporally. Within meters, substrate size, shading from forest cover, and water depth can change dramatically. Likewise, stream discharge can rapidly increase an order of magnitude. Such heterogeneity is reflected in the spatial and temporal variation of diverse macroinvertebrate stream assemblages (Heino et al. 2004). Related to this heterogeneity has been controversy regarding the effects of predators on the abundance of their prey.

The broad objective of this project was to investigate the roles of trout as predators in streams, a topic that seemed quite clear to me following my master's research on larval salamanders (Barr 2000, Barr and Babbitt 2002). The scope of my interest, previously viewed narrowly through salamander-goggles, was expanded by the series of PI models that addressed the remarkable variation in results among stream predation studies. Cooper et al (1990) and Sih and Wooster (1994) suggested that the variation among studies was largely due to the movement of prey into and out of experimental arenas (typically small).

However, Englund's (1997) model suggested that at a large spatial scale, movement rates have little relevance. The study with the largest experimental arenas that effectively established trout and fishless stream reaches used 35 m sections and indicated the strong influence of prey movement (Forrester 1994). By using much larger stream reaches and replicating across streams rather than with short segments in a single stream, I aimed to more effectively address the impacts of trout on prey abundance and activity in a more realistic arena than previous research.

My results show that trout have little impact on macroinvertebrate assemblages, at least in this mountainous New Hampshire stream system. Among the many macroinvertebrate taxa, density tended to vary with time and space rather than with trout presence. Likewise, in all but a few taxa, behavioral drift responses to trout were not evident; invertebrate drift activity varied temporally and was nocturnal for nearly all taxa. In contrast to invertebrates, salamanders were less abundant with trout. They also decreased their surface activity, changing from aperiodic in fishless streams to mostly nocturnal in streams with trout.

Despite the large-scale nature of the field experiment, the inference space of the results remains rather small. The temporal and spatial scales of this project exceed those of most other projects on the topic. Extrapolating from the 9 study sites to other low-order streams in the White Mountains and throughout the northern reaches of the Appalachian

Mountains in New York, Vermont, New Hampshire, and Maine seems reasonable. However, species composition, climate, and geology are a few among many factors that can affect interactions among species. Systems with greater canopy openness and autochthonous production, such as fairly well studied New Zealand and Colorado Rocky Mountain streams, are subject to different mechanisms. Finer distinctions may come with smaller changes in climate, stream substrate, and species composition if we move south along the Appalachian Mountains. How do salamanders persist with other fish species? Sculpin (*Cottus sp.*) are benthic and nocturnal foragers; do they affect salamander abundance, activity, and prey capture differently than trout? How does a larger suite of predators affect salamanders and macroinvertebrates?

It is interesting that trout seem to have a strong impact on salamanders but little on macroinvertebrates. The difference may be related to a number of factors, including abundance, size (thus conspicuousness), demography (immigration/emigration, birth/death rates), indirect effects, and statistical power. Regardless, the literature suggests that larger, intermediate predators are affected by fish predation more so than are smaller invertebrates (Meissner and Muotka 2006). I rarely found large stoneflies, a commonly studied predator of smaller invertebrates, but salamander larvae may occupy a niche similar to large stoneflies. They are both benthic feeders that respond to fish

presence and seem to illicit a behavioral response by their prey. Research on the interactions among stoneflies, fish, and their shared prey may serve as an effective model for studies aimed at expanding our understanding of the roles of salamanders as predators and prey in streams.

Like research on stoneflies, my small-scale laboratory experiment suggests that as predators, trout and salamanders show interesting interactions that, beyond the direct impacts on salamander abundance and activity, have implications for invertebrates and trout fisheries. The behavioural interactions among trout, salamanders, and their shared invertebrate prey suggest that when together, salamanders eat fewer prey but trout eat more. Combined, such interactions represent a complex suite of processes that are likely important in stream systems and may be an important factor influencing our ability to measure impacts of trout on macroinvertebrate density. The lower abundance of salamanders in trout streams likely has a positive, indirect trophic effect on stream invertebrates; however, the enhanced predation rates of trout in the presence of salamanders may compensate for reduced salamander consumption. Further research on larval salamanders in streams seems justified.

The original impetus for this research came from the 3 PI models. This research project did not strongly support nor reject the validity of the models, but as most research projects do, leaves me with more questions

unanswered. The models make sense and are supported by research at a range of spatial scales. However, that range of scales rarely reaches 10 m or spans more than a single season. In how many stream systems do predators have a dominant or even measurable effect on prey abundance? In the context of a stochastic system with a variable flow regime and great diversity of microhabitats (substrate, depth, canopy cover, predation intensity), how importantly does predation typically rank? Continued small-scale experiments that focus on few taxa in controlled situations may identify measurable effects of trout and salamander on invertebrate abundance and activity. However, the translation of such patterns to natural systems may be difficult (Peckarsky et al. 1997). The same heterogeneity that makes large-scale field projects difficult and labor intensive is what makes them so useful. Such heterogeneity often obscures patterns that are clear or spurious at smaller temporal and spatial scales.

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APPENDIX

UNIVERSITY OF NEW HAMPSHIRE

Office of Sponsored Research
Service Building
51 College Road
Durham, New Hampshire 03824-3585
(603) 862-3564 FAX

LAST NAME	Babbitt	FIRST NAME	Kim
DEPT	Natural Resources Department, 226 James Hall	APP'L DATE	6/28/2001
OFF-CAMPUS ADDRESS (if applicable)	Natural Resources Department, 226 James Hall	IACUC #	010604
PROJECT TITLE	The functional role of trout and larval salamanders as predators in streams		

All cage, pen or other animal identification records must include your IACUC Protocol # as listed above.

The Institutional Animal Care and Use Committee reviewed and approved the protocol submitted for this study under Category 1 on Page 3 of the "Application for Review of Animal Use or Instruction Protocol" - the program involves either no pain or potentially involves momentary, slight pain, discomfort or stress. The IACUC made the following comments on this protocol -- *comments* are usually minor editorial changes or clarifications that do not affect approval status (unlike contingencies, which require investigator action for initial or continuing approval):

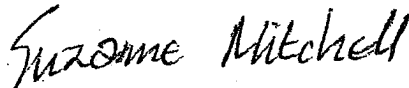
1. In Section I, F (proposed animal involvement), the Committee added "0" under Average Daily Inventory of Animals for both species.

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please note: Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. *Participation is mandatory* for all principal investigators and their affiliated personnel, employees of the University and students alike. A Medical History Questionnaire accompanies this approval; please copy and distribute to all listed project staff who have not completed this form already. Completed questionnaires should be sent to Dr. Gladi Porsche, UNH Health Services. Thank you.

If you have any questions, please contact either Van Gould at 862-4629 or Julie Simpson at 862-2003.

For the Institutional Animal Care and Use Committee,



Suzanne H. Mitchell, Ph.D.
Chair

cc: File